Sensitivity of Taphonomic Signatures to Sample Size, Sieve Size, Damage Scoring System, and Target Taxa

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The sensitivity of taphonomic signatures to a battery of common sampling and analytic procedures is tested here using modern bivalve death assemblages from the San Blas Archipelago, Caribbean Panama, to determine (a) the magnitude of methodological artifacts and, thus, the comparability of taphofacies patterns among studies; and (b) the most efficient and robust means for acquiring damage profiles (taphonomic signatures) of death assemblages both ancient and modern. Damage frequency distributions do not stabilize below sample sizes of 120–150 individuals. Using damage to the >8 mm portion of the assemblage as a baseline (interior damage only, fragments included), it is found that qualitative *trends among environments (higher damage levels in reefal skeletal gravel versus mud) and the rank-order importance of taphonomic variables per environment (intensity of damage from encrustation, boring, fine-scale alteration, edge-rounding, fragmentation) are robust to most methodological decisions. The exception is the use of target taxa: of three genera tested, only one was sensitive to the same suite of environmental differences as the total-assemblage, and taxa had disparate rank-ordering of variables. In contrast to the general robustness of qualitative trends, quantitative damage levels are affected significantly by methodology. Specifically, the measured frequency of damage is generally lower for finer size fractions and finer sieve sizes, for whole shells versus fragments, for taxonomically well-resolved specimens, for infaunal versus epifaunal species regardless of mineralogy, and for interior surfaces versus exterior or total surface area of shells. Full frequency-distribution data on states of taphonomic damage are most powerful for differentiating samples, but if single-value metrics are desired, the frequency of high-intensity damage is more powerful—and shows less between-operator variance—than presence-absence data or average damage state. To maximize the detection of damage and of between-environment differences in taphonomic signature, and to foster between-study comparisons, the following are recommended: (1) analysis of discrete size-fractions rather than broad spectra and, in particular, the separate treatment of coarse size fractions (>4 mm); (2) examination of complete assemblages (fragments as well as whole specimens; all species or broad subsets of species rather than select taxa); (3) variables scored independently (e.g., encrustation v. boring) rather than grouped into summary grades; and (4) evaluation of rank-ordering of variables in plots of threshold damage profiles as a complement to ternary taphograms.*

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INTRODUCTION

For the last fifteen years, taphonomists have focused increased effort on quantifying variation in post-mortem damage among environments. The primary aim of such taphofacies analysis (*sensu* Speyer and Brett, 1986) has been to improve the quality of paleoenvironmental interpretations by considering the state of preservation of organic remains, including patterns of damage to skeletal hardparts and styles of skeletal concentration. An outgrowth and complement to sedimentary microfacies analysis (e.g., Pilkey, 1964; Pilkey et al., 1969, 1979; and see Flügel, 1982), this information also can help to recognize exotic material (damage patterns distinct from indigenous material; e.g., Davies et al., 1989; Miller et al., 1992), to rank the importance of taphonomic variables (by relative intensity or frequency of damage in assemblage; e.g., references in Table 1, and see below), and, inferentially, to estimate the facies-by-facies reliability of paleobiologic information, under the assumption (following Johnson, 1960) that assemblages dominated by well-preserved skeletons are less time-averaged or otherwise modified than those with high post-mortem modification (and see review by Parsons and Brett, 1991).

"Taphonomic signatures" (Davies et al., 1989) now have been documented for a variety of groups in both modern and ancient systems (for actualistic examples, see Nebelsick, 1999, for echinoids; Llewellyn and Messing, 1993, for crinoids; Pandolfi and Greenstein, 1997, and Perry, 2000, for corals; Smith and Nelson, 1994, for bryozoans; Martin and Liddell, 1991, for foraminifera; Gastaldo et al., 1987, for macroflora). Marine mollusks have received the most attention, but no consensus has emerged on taphofacies methodology. For example, of 20 actualistic molluscan taphofacies analyses (Table 1), 12 different sieve sizes have been used, and there has been a similarly high degree of variation in the taphonomic variables scored (e.g., fragmentation, rounding, boring), in how damage states are quantified (e.g., number of "grades" per variable and grade definition), in the portion of the death assemblage examined, and in methods of data analysis. This diversity is natural given the youth of the quantitative taphofacies approach, but makes comparison and synthesis of results extremely difficult and, thus, reduces the collective value of this effort.

Here, as a guide for future studies, the sensitivity of molluscan taphonomic signatures is evaluated relative to methodological decisions during sampling, data-collection, and data-analysis. By applying a battery of methods to a single set of samples, in this instance bivalve death assemblages from subtidal mud, sand, and shell gravel across a small fringing reef in the San Blas Archipelago of Carib-

TABLE 1—Summary of methods used in actualistic molluscan taphofacies studies. * each taphonomic variable scored macroscopically (10×) and analyzed independently, unless otherwise noted; damage scored as presence-absence (''±'') or according to the degree of damage to the shell (''damage state''). ''Summary grades'' are damage categories for individual shells based on multiple rather than single variables.

Study	Sieve size mm (size fractions tested)	Inclusion of fragments & specimens not identifiable to species-level	Set(s) of taxa analyzed	Surfaces examined & compared	Taphonomic variables	Form of data for individual shells*	Description of assemblage, & analysis of differences among assemblages
US Atlantic continental shelf (Pilkey et al., 1969)	2 (2–4)	Included fragments, both identifiable & unidentifiable	Total shell material in size fraction, dominantly molluscan	Total only	Fragmentation, rounding, discoloration	± fragmentation; damage state for other variables	Maps of % damage
Puerto Rico continental shelf (Pilkey et al., 1979)	1 (1–2)	Included fragments, both identifiable & unidentifiable	Total shell material in size fraction, dominantly molluscan	Total only	Rounding, luster	Damage state; also 3 summary grades (old dull, old polished, fresh original)	Histograms of % damage
Georgia shelf palimpsest sand (Frey & Howard, 1986)	2.5	Only taxonomically identifiable fragments included	All mollusks	Total only	Encrustation, boring; retention of original color, gloss; presence of ligament or periostracum	2 summary grades (''old-new''); encrustation & boring treated separately	Line-graphs of new:old valve ratios, and % ± damage
Georgia longshore tidal channel and nearshore shelf (Henderson & Frey, 1986)	1.5	Included fragments	All mollusks	Not specified	Size-sorting, % articulated, right-left ratios of bivalves; retention of original color, gloss; presence of ligament or periostracum	2 summary grades (''old-new''); ± data for articulation	Line-graphs of new:old, right:left, and % articulated specimens
Sonora tidal flat (Fürsich & Flessa, 1987	3	Damage to whole, identifiable shells only	6 target genera (3 infaunal bivalves, 2 epifaunal gastropods, 1 infaunal echinoid)	Interior only	Abrasion, luster, color, fragmentation dissolution, boring, encrustation	Sum of ordinal damage states	Bivariate plots and histograms of summed scores and of full-frequency data on states
Texas tidal inlet (Davies et al., 1989)	2 (2–4, 4–8, 8–16, >16)	Included fragments, both identifiable & unidentifiable (tested effects)	All mollusks	Total; interior v. exterior; 8 morphologic subareas	Dissolution, fragmentation, abrasion include edges, ''biotic'' (includes predatory drillholes), size-sorting	Damage state	Tables of %-state data and MANCOVA results
Texas continental shelf above storm wavebase (Staff & Powell, 1990)	4 (4–12, >12)	Included fragments, both identifiable & unidentifiable (tested effects)	All mollusks; 2 infaunal target spp	Total; interior v. exterior; 8 morphologic subareas	Disarticulation, fragmentation, dissolution, abrasion include edges, ''biotic'' (includes predatory drillholes), right:left & size-sorting	Damage state	Tables of %-state data and MANCOVA results
Massachusetts tidal flat (Meldahl & Flessa, 1990)	6	Damage to whole specimens only	single infaunal bivalve	Total only	Fragmentation, edge rounding, exterior abrasion, alteration of muscle scars, boring, encrustation	± damage	Histograms and cluster analysis of %-± data; multi-dimensional scaling to identify pathways of damage accrual

TABLE 1—Continued.

Study	Sieve size mm (size fractions tested)	Inclusion of fragments & specimens not identifiable to species-level	Set(s) of taxa analyzed	Surfaces examined & compared	Taphonomic variables	Form of data for individual shells*	Description of assemblage, & analysis of differences among assemblages
Sonora tidal flat (Feige & Fürisch, 1991)	3	Damage to whole, identifiable shells only	All mollusks; plus separate samples of 6 target mollusk genera (4 infaunal, 2 epifaunal)	Interior only	Loss of ornament (abrasion + bioerosion), loss of color, encrustation, boring, fragmentation, articulation, right:left sorting, dissolution, maceration	Damage state	Bivariate plots of average state (alteration index) ± data, stacked bargraphs of full-frequency data
Texas continental slope cold seep (Callender & Powell, 1992)	1	Included fragments, both identifiable & unidentifiable (tested effects)	All mollusks; target species from each biofacies	Total; interior v. exterior; 8 morphologic subareas	Fragmentation, articulation, right:left & size-sorting, presence of periostracum, "dissolution", precipitation, edge condition, abrasion, "biotic interactions"	Damage state	Tables of %-state data, Chi square & nested MANOVA results
Texas cold seep, nearshore shelf, & tidal inlet (Callender et al., 1992)	4 (4–9, 9–14, 14–19, 19–24, >24)	Included fragments, both identifiable & unidentifiable	All mollusks	Total; interior v. exterior; 8 morphologic subareas	Dissolution, abrasion, edge rounding, fragmentation, biotic interactions, articulation, right:left ratios, size-sorting	Damage state	Tables of %-state data Chi square results
Virgin Islands carbonate shelf (Parsons, 1989, 1993)	5	Included fragments	All mollusks	Total only	Disarticulation, fragmentation, encrustation, bioerosion, root etching, edge rounding, abrasion, color loss	Damage state	Bar-graphs of frequency data, discriminant analysis of average states
Baja California cheniers (Kowalewski et al., 1994)	12.5	Included fragments	Single infaunal bivalve species	Total except interior v. exterior luster	Bioerosion, encrustation, fragmentation, cracking, exterior peeling, edge condition, luster, state of interior features; size-sorting, articulation, right:left	Damage state	Ternary taphograms of full-frequency data, multivariate analysis of average states (PCA, CVA); cluster analysis & binomial tests of pooled samples
Germany, Baja & Sonora tidal flats (Kowalewski et al., 1995)	30 mm mean size	Included fragments	1–2 infaunal bivalve species per study area	Total except interior v. exterior luster	Fragmentation, surface abrasion, bioerosion, encrustation, luster & color loss	Damage state	Ternary taphograms of full-frequency data

TABLE 1—Continued.

Study	Sieve size mm (size fractions tested)	Inclusion of fragments & specimens not identifiable to species-level	Set(s) of taxa analyzed	Surfaces examined & compared	Taphonomic variables	Form of data for individual shells*	Description of assemblage, & analysis of differences among assemblages
Norway low-tide beach and Sonora intertidal flat (Cutler & Flessa, 1995)	30	Included fragments	5 spp Norway, 7 comparable spp Sonora	Interior only	Microbioerosion, dissolution/ maceration, precipitation textures @ 40× & 100× magnification	± damage	Bar-graphs of %-± data
Sonora tidal flat (Cutler, 1995)	6	Whole, identifiable shells only	2 infaunal bivalve spp	Interior only	Bioerosion, abrasion, dissolution	± damage	Bar-graphs of %-± data
Florida carbonate shelf (Dent, 1996)	2	Included fragments	15 most abundant mollusks; 2 epifaunal & 1 infaunal target spp	Total only	Abrasion, clionid boring, color loss, encrustation, edge rounding, fragmentation, fine-scale alteration	Damage state	Bar-graphs & ternary taphograms of frequency data; cluster analysis of average state
Baja California bay (Meldahl et al., 1997b)	15	Whole disarticulated shells only	Infaunal bivalves	Interior only	Color loss, bioerosion, encrustation, fine-scale alteration	4 summary grades	Bivariate plots of average state (Taphonomic Grade Index)
San Blas Archipelago, Panama inner shelf (Best, 2000)	8	Included fragments, both identifiable & unidentifiable	All bivalves; infaunal v. epifaunal; calcitic v. aragonitic; 1 target infaunal bivalve	Interior only; comparison of 3 interior microstructural sectors	Disarticulation, fragmentation, boring, encrustation, fine-alteration, edge modification, alteration colors	Damage state	Stacked bar-graphs of frequency data; binomial confidence intervals; bootstrapping; contingency; non-metric multi-dimensional scaling
Bocas del Toro, Panama lagoon (Best & Kidwell, 2000a, 2000b)	8	Included fragments, both identifiable & unidentifiable	All bivalves; infaunal v. epifaunal; calcitic v. aragonitic	Interior only	Disarticulation/ fragmentation, boring, encrustation, fine-alteration, edge modification	Damage state	Bar-graphs of high-threshold damage; binomial confidence intervals
San Blas Archipelago, Panama inlet (this study)	2 (2–4, 4–8, >8)	Included fragments, both identifiable & unidentifiable (tested effects)	All bivalves; infaunal v. epifaunal; 3 abundant target spp	Total, interior v. exterior	Disarticulation/ Fragmentation, boring, encrustation, fine-alteration, edge modification	Damage state	Bar- and line-graphs of high-threshold, ±, and average state data; stacked-bar and ternary taphograms of full-frequency data; binomial confidence intervals

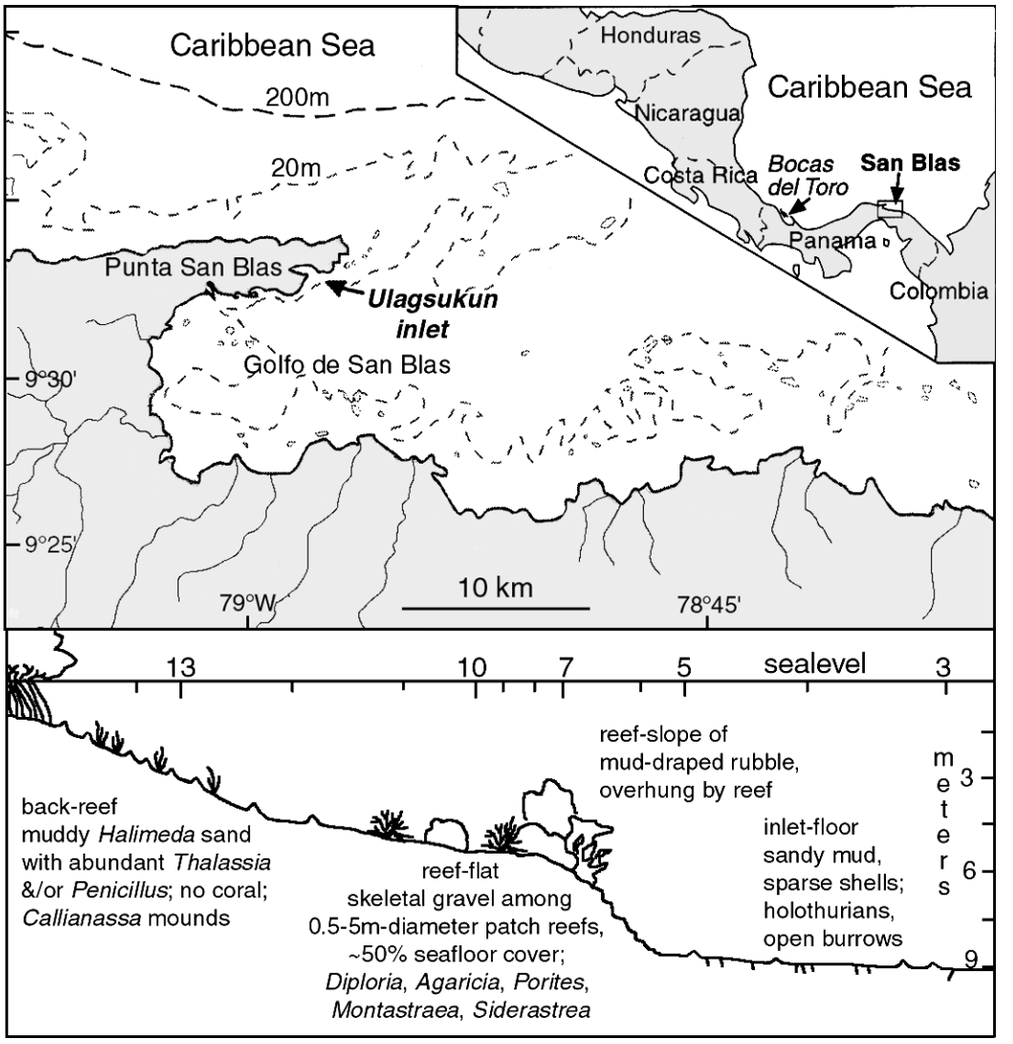

FIGURE 1—Bivalve death assemblages were sampled from the top 10 cm of sediment along a cross-reef transect in the cul-de-sac Ulagsukun inlet on the lee-side of the Punta San Blas peninsula, Caribbean Panama (site numbers along top edge of cross-section, which is drawn without vertical exaggeration).

bean Panama, it is possible to (a) quantify the magnitude of methodological artifacts in taphofacies patterns, and (b) identify the most efficient and robust means for acquiring damage profiles of death assemblages.

STUDY AREA

The San Blas Archipelago lies along the Caribbean coast of eastern Panama at ~9.5° N between the Canal and the Colombian border (Fig. 1). Samples were collected from a transect of reef-flat, back-reef, and down-slope sediments in the low-energy head of a small, V-shaped, mangrove-rimmed cul-de-sac (Ulagsukun inlet) on the lee coast of the Punta San Blas peninsula at the western end of the Archipelago (9° 33.02′N, 78° 59.73′W). This transect includes a fieldsite from the work of Best (2000; site 95SB053; see her more detailed map), where sediment type, rates of experimental shell degradation, radiocarbon-calibration of time-averaging, and pore-water geochemistry are all being analyzed (Ku and Walter, 1998; Best et al., 1999). For a general treatment of sediments in the San Blas Archipelago, see Best (2000, Chapter 2).

The mouth of Ulagsukun inlet is edged on both sides by a fringing reef of high coral diversity, which continues around the end of the Punta San Blas (Fig. 1). Coral communities extend into the inlet as it narrows and shallows along a somewhat sinuous course. The inlet appears to be a relict stream valley, flooded during Holocene sealevel rise, with a deep, central channel and relatively flat subtidal shoulders, whose edges support the major coral growth (Best, 2000, Chapter 2). The inlet is very low-energy away from its mouth, protected by its sinuous plan and narrow, reef-constricted mouth from squalls on the Golfo, and protected by the peninsula from Caribbean storms.

Reef development within the inlet becomes patchier with distance from the mouth, and at the sampled tran-

TABLE 2—Taphonomic variables and damage states used to score bivalve shells in this study (under 10× magnification; modified from Best and Kidwell, 2000a).

Variable	0 = No Damage	1 = Low Damage	2 = High Damage	Notes
Encrustation	None	Covering <10% shell area	Covering ≥ 10% area	Total coverage by all taxa
Boring	None	Affecting <10% shell area	Affecting ≥ 10% area	Non-predatory borings only
Fine-Scale Surface Alteration	None	Dull or chalky	Both chalky & pitted, or eroded	For shell interiors, area outside the pallial line only
Edge Modification	None	Chipped	Rounded	Commissural edge only
Fragmentation	Valve still articulated	Whole but disarticulated	Large or small fragment	

sect consists of a ~7 meter-wide zone of live coral and skeletal gravel within a predominantly fine-grained siliciclastic environment (Fig. 1; no vertical exaggeration in transect cross-section). Siliciclastic sediment is shed from the Punta San Blas peninsula (see Chapter 2, Best, 2000). *Halimeda*-sand-rich mud with reef-derived coral debris accumulates on the narrow, gently sloping back-reef seafloor along the mangrove shoreline. These back-reef sediments are sparsely vegetated by patches of *Halimeda, Penicillus,* and *Thalassia,* and are heavily burrowed by callianassid shrimps, which produce abundant mud-draped mounds on the seafloor and shelly sand-filled burrows to 50 cm or deeper in cores (*Halimeda* constitute 85 wt-% of > 2 mm bioclasts; sand is ~50:50 mix of siliciclastic and bioclastic grains). In the transition zone to the reef, *Thalassia* is replaced by scattered corals, mostly small ≤ 50 cm-diameter *Porites* and *Diploria.* Reef development occurs along the 5–6-m deep edge of this marginal shoulder and covers ~50% of the seafloor at the line of transect. The central reef zone consists of isolated coral heads (*Montastraea, Diploria*), small *Porites*-dominated thickets, and polytaxic patch reefs up to 5 m diameter, with generally high live-coral coverage. Sediments within this reef-zone are strongly discolored (dark gray and rust) gravel of coral and molluscan skeletal debris. *In situ* coral patches and reef-derived coral rubble decrease in size and abundance down the steep, mud-draped reef-slope (~45 degrees; transect in Fig. 1 is drawn without vertical exaggeration). This slope has an abrupt transition with the flat central floor of the inlet (10.5 m maximum depth), which is characterized by unvegetated, highly bioturbated, soft organic-rich clayey mud (3.0 wt-% TOC), with admixed bioclastic sand, sparse low callianassid mounds, and abundant live holothurians and open burrows (1–2 cm diameter) of unknown origin. Site 5 is located on this flat floor near the base of the reef-slope, and site 3 near the channel axis. At site 3, the mud contains only trace gravel >2 mm, which is composed of equal quantities of *Halimeda* (transported from back-reef, along with mangrove litter), mollusk shells, and unidentified bioclasts.

METHODS

A series of ~5-liter surface sediment samples were taken along this transect on SCUBA in January, 1997, using a large rectangular plastic scoop to excavate the top 10 cm of the seafloor (Fig. 1B). Each sample, which had been placed in a heavy polypropylene bag for retrieval, was subsampled for quantitative grain-size analysis, with the remainder of the bulk sediment wet-sieved in the field through a 2 mm plastic mesh. These skeletal residues were later washed with fresh water, air dried, and gently resieved through 2, 4 and 8 mm mesh in the lab.

Bivalve shells and fragments were picked from splits of samples from five sites along this transect: back-reef *Halimeda*-rich muddy sand (site 13); skeletal gravel from the central and outer edge of the reef flat (sites 10 and 7; approximate replicates); shelly mud on the inlet-floor near the base of the reef-slope (site 5); and clayey mud on the distal inlet-floor (site 3; experimental site 53 of Best, 2000). Bivalve shell abundance, especially specimens >8 mm, was relatively low at site 3 and, hence, that sample was augmented with material collected from the same area in previous years. In general, few bivalve specimens were larger than 2 cm in any environment; thus, shell size was narrowly constrained even within the >8 mm portion.

Replicate samples were examined from the reef-flat (sites 7 and 10) because earlier studies found highest among-sample variability within facies that include significant hard substrata (Best and Kidwell, 2000a). Site 7 sediment was adjacent to and slightly down-slope from a patch of small (≤50 cm) *Montastraea annularis* colonies, and was very coarse with just a thin (few mm) veneer of mud on the surface (Fig. 1). Site 10 was rubble between a 3–4 m diameter patch reef of *Agaricia, M. annularis,* and *M. cavernosa,* and a 2m-diameter reef of *Agaricia* and *M. annularis,* in the core of the reef-flat. Reef-slope site 5 and back-reef site13 are lithologically very similar to each other in containing significant mud and reef-derived coral debris, but are not environmental replicates.

Each specimen was identified taxonomically to species level when possible, and the degree of damage was scored for five macroscopic taphonomic variables, using 10 × stereoscopic magnification: encrustation, boring, fine-scale surface alteration, commissural edge modification, and disarticulation/fragmentation. In scoring damage, the operational criteria of Best and Kidwell (2000a; very similar to those of previous workers, Table 1) were followed, but the degrees of damage were reduced to three states per variable (Table 2). Damage to interior and exterior surfaces of shells was scored separately, unless the specimen was too damaged for this distinction to be made. *Boring* refers to any non-predatory penetration of the shells, and is primarily by clionid sponges. Dominant macroscopic *en-*

crusters are serpulid worms and bryozoans (both runner and sheet forms). Although not quantified, the taxonomic composition of the fouling community was similar to that in carbonate and siliciclastic habitats in the Bocas del Toro area of Caribbean Panama (Best and Kidwell, 2000a; Fig. 1). *Fine-scale surface alteration* denotes macroscopic (10×) dulling (loss of luster), chalkiness, pitting, and erosion or exfoliation of the original shell surface. Only with SEM can this fine-scale alteration be interpreted confidently as the product of microbioerosion, mineral dissolution, organic-matrix maceration, and/or physical plucking (SEM of San Blas bivalves by Best, 2000; and see Cutler, 1995; Cutler and Flessa, 1995); thus, these process-terms are not used. To control for microstructure and *in vivo* effects, damage to shell interior surfaces was scored only for the area outside the pallial line (OPL), which is the "outcrop area" of the outer shell layer; damage to shell exteriors was based on the entire exterior surface (also composed of the outer shell layer). This contrasts with previous workers who have treated the entire shell as a unit, or have subdivided it into standard areas related to shell shape (e.g., Davies et al., 1989; others in Table 1). *Edge modification* refers to the shell commissure only, and not edges produced by fragmentation. SEM indicates that bioerosion (microboring, grazing) rather than physical abrasion is the key process of rounding in these environments (Best, 2000; and see Best and Kidwell, 2000a). Edge chipping is a less severe modification of the commissure and probably is generated by predators, especially crabs; some chipping may be from handling during collection, shipping, and washing. Edge-thinning was negligible. *Fragmentation* appears to be largely the product of predation, as it is high in all environments despite their low physical energies. Differences among assemblages were evident during collection; thus, it is not believed that fragmentation is greatly affected by handling. Fragments without hingelines ("minor" fragments of Staff and Powell, 1990) were treated the same as those including hingelines. Although some workers treat it as a separate variable, disarticulation is treated here as a state within the fragmentation category (Table 2).

To permit analysis of co-occurring features on individual shells and facilitate re-examination, specimens were given unique identification numbers and archived (in shallow boxes using double-sided tape).

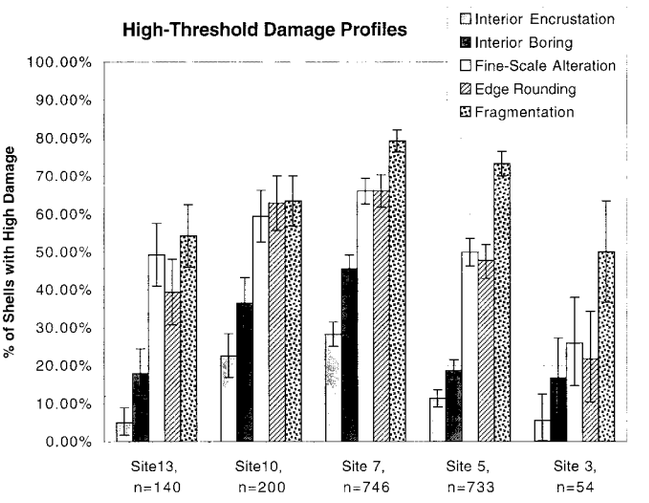

FIGURE 2—Damage profiles for sites based on the frequency of high-damage states in the >8 mm size fraction of the complete bivalve death assemblage. These profiles are the baseline for evaluating different methods of analysis, and reflect damage to shell-interiors of all bivalve specimens, including fragments, epifaunal as well as infaunal species, and specimens that cannot be identified to species or genus level. Note similarity among sites in rank-order importance of the five variables, but quantitative differences among environments in the frequency of highly damaged shells (95% binomial confidence intervals; a variable whose value lies outside the C.I. of another is significantly different; sites 7 and 10 are replicate samples of the same reef-flat environment).

RESULTS

Baseline Damage Profiles

Damage to shell interiors in the >8 mm size fraction was used to establish a baseline damage profile for each bivalve death assemblage. All specimens of bivalve origin were assessed, including fragments and specimens that could not be resolved to species or genus level. The "taphonomic signature" of each assemblage is expressed as a high-intensity damage profile (bar-graphs of Fig. 2), with each variable (bar) treated independently and only the frequency of damage above a certain threshold intensity plotted ("threshold damage profile"). Here, the height of each bar indicates the percentage (frequency) of shells in the sample that exhibit the highest degree of damage for that variable (as defined in Table 2), with 95% binomial confidence intervals following Raup (1991). A variable whose value lies outside the confidence interval (C.I.) of another is significantly different.

Qualitatively, reef-flat shell gravels (replicate sites 7 and 10) exhibit highest overall damage levels, declining to intermediate levels in muddy shell-gravel (back-reef site 13 and reef-slope site 5), and the lowest observed levels in shell-poor mud (inlet-floor site 3). The signatures of these sites show high similarity in the rank-ordering of taphonomic variables—in all profiles, encrustation < boring < fine-scale damage ≤ edge rounding ≤ fragmentation. Quantitatively, however, the profiles differ significantly. Pairwise tests indicate that, with the exception of the site 3/13 comparison (the two sites with smallest sample sizes), profiles differ in 3, 4, or all 5 tested variables (Table 3). Sites that are most similar in environmental features are least dissimilar in damage profile: reef-flat replicate sites 7 and 10 differ in only 3 variables, as do reef-rubble-rich sites 5 and 13.

In the sections that follow, baseline damage profiles are evaluated with respect to different methods of data collection and analysis.

Use of Finer Size Fractions and Sieve Sizes

For all variables except fragmentation, there is a significant size-fraction effect on taphonomic damage: in both end-member assemblages (site 7 shell gravel and site 3 mud), the 4–8 mm size fraction has the same or lower frequency of high-damage shells than >8 mm fraction, and

TABLE 3—Site by site comparison of high-intensity damage profiles of Figure 2, based on damage to the interior surfaces of shells >8 mm. In each cell, the results are listed as a string for the 5 test variables: encrustation, boring, fine-scale alteration, edge modification, and fragmentation. • = frequency of damage significantly different at 0.95 C.I; n = not significantly different.

Site	10	7	5	3 (n = 54)
13 (n = 140)	• • • • •	• • • • •	• nn • •	nn • • n
10 (n = 200)		• • nn •	• • • • •	• • • • •
7 (n = 746)			• • • • •	• • • • •
5 (n = 733)				• n • • •

the 2–4 mm fraction has a significantly lower frequency than either of the coarser fractions (Fig. 3A-B, Table 4). This effect is most pronounced for boring and encrustation. (If damage to exterior shell surfaces is used, this size-fraction effect is even stronger, especially in shell-gravel of site 7, where encrustation, boring, and fine-scale alteration all exhibit disparities between size fractions of up to 45 percentage points.) In contrast, fragmentation in the 2–4 mm fraction tends to be as high as, or higher than in, coarser fractions.

Because fine fractions comprise far more specimens than coarse fractions in bulk samples, the taphonomic signature of the finest size-fraction is expected to dominate the overall damage profile of an assemblage. To test for this in San Blas samples, data were pooled from size-fractions to simulate alternative sieve sizes, and it was found that fine sieves do yield lower damage profiles than coarse sieves (Fig.3C-D). [Note: data on the 2–4 and 4–8 mm size fractions are based on subsamples of the total fine-material (1/10 to 1/3 of material actually associated with >8 mm specimens); this was compensated for in pooling data]. Using a 4 mm rather than an 8 mm sieve has a relatively small effect on damage profiles for site 7 shell gravel: only encrustation and fragmentation shift significantly (confidence intervals are too large for the >8 mm fraction to determine an effect at site 3). In contrast, adding the 2–4 mm fraction to the others to simulate a 2 mm sieve shifts most variables to significantly lower values at both sites.

Thus, the use of finer sieves reduces the measured frequency of high-intensity damage in assemblages. Rank-order of variables is conserved, however, and among-site differences in profiles are still evident (Fig. 3C-D).

Sample Size

Samples yield highly variable numbers of specimens, which may be insufficient (or, at the other extreme, overkill) for confident determination of taphonomic signatures. Cumulative sampling curves, plotted during data collection from successive sets of ten specimens ("collection curves"), indicate that the true proportions of damage in the assemblage can be approximated with a sample size of 50 specimens, but that generally 120–150 specimens are needed to confidently establish damage profiles for the five variables tested here. Figure 4 presents the results for the 2–4 mm size fraction at two end-member sites (reef-flat shell gravel site 7, and inlet-floor mud site 3; compare to Fig. 3C-D).

Increasing the sample size above the 150-specimen threshold does not change the measured %-frequency of damage significantly, but narrows the confidence intervals. In this study, the very large sample sizes for some sites permitted statistical power to be maintained when analyzing subsets of the total assemblage, e.g., when targeting specific taxa or subgroups of taxa (see later sections).

Analysis of Total Shell Surface Versus Interior-Only

The interior and exterior surfaces of most shells exhibit the same degree of damage from boring, encrustation, and fine-scale surface alteration (cells along diagonals in contingency Table 5). When damage on the two surfaces is unequal, however, exterior surfaces are at least twice as likely to carry the greater damage (upper right cells in Table 5). Some of this difference may be truly taphonomic; for example, if the mineralogy, microstructure, or topography of the shell exterior is more prone to attack by post-mortem physical, chemical, and biological processes. However, much of the "excess" damage to shell exteriors may accrue during the life of the bivalve, especially for taxa that are epifaunal or lack a protective outer periostracal layer. Disparity in frequencies of high-damage between shell interior and exterior surfaces is evident in all size fractions (Table 4).

Scoring the extent of shell damage to the total shell surface (interior plus exterior; this is the procedure in most taphofacies analyses, Table 1) should yield higher %-frequencies of damage in an assemblage than when damage is scored on the basis of interior surfaces alone. This is indeed the case in San Blas assemblages for high-intensity damage profiles, and these differences are significant in all environments except inlet-floor mud (site 3, low n; Figure 5). This effect is evident in all size-fractions of the bivalve death assemblage down to 2 mm.

Despite the inflationary effect on %-frequency values, among-site differences in damage profiles are largely robust: (a) edge-rounding and fragmentation are completely unaffected; (b) the *rank-order* importance of the three affected taphonomic variables is unchanged (frequencies of fine-scale alteration exceed those of boring, which exceed those of encrustation, regardless of whether total shell surfaces or interiors-only are scored); (c) both scoring methods detect the same taphonomic trends among sites; and (d) pairwise differences in damage levels among environments are still statistically significant (sole exception is the lack of difference in boring levels between sites 3 and 5 for shell interiors).

Thus, although damage to shell exteriors has ambiguous origins and systematically increases measured values of damage, its inclusion does not obscure among-habitat differences that are strictly taphonomic in origin. This finding has particular relevance to studies in lithified sediments, where it is commonly difficult to examine shell interiors.

Exclusion of Fragments

In the >8 mm size fraction (interior surfaces only), fragments yield higher frequencies of all types of damage than

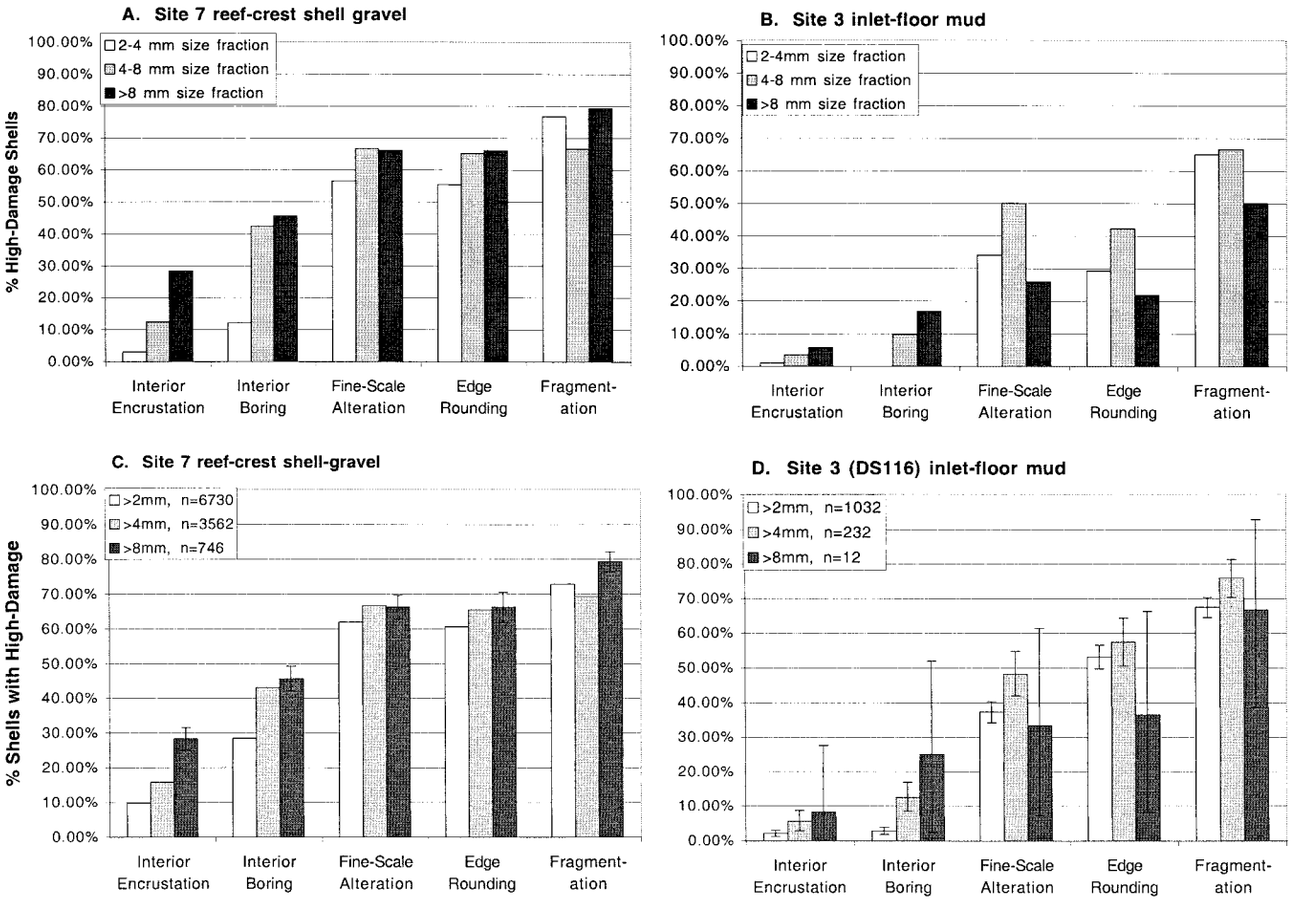

FIGURE 3—Effect of size fraction (**A-B**) and sieve size (**C-D**) on damage profiles for site 7 shell gravels and site 3 muds; 95% binomial C.I.s, which are too small to plot for all bars in site 7 data. When pooled, the far more numerous and typically less damaged specimens of finer size fractions reduce the overall frequency of damage in the assemblage. Pooling the 4–8 mm and >8 mm fractions has small effect on damage profiles (only encrustation and fragmentation change significantly at site 7; no differences at site 3); adding the 2–4 mm fraction has a stronger effect on most variables at both sites.

whole shells, and these differences are significant in all environments tested except site 3 mud (Fig. 6). In San Blas assemblages, where fragments constitute 50–80% of specimens in bivalve death assemblages (Fig. 2A), the exclusion of fragments yields damage profiles significantly lower than if all bivalve material is scored (generally by 10 or more percentage points per variable). The rank order of variables (shape of the profile) is conserved.

Thus, the intensity of perceived damage in the death assemblage depends on the proportion of whole and broken shells. Profiles based on whole shells alone will have damped values compared to total-assemblage profiles, but

TABLE 4—Percentage-point difference in the frequency of high-damage states between the >8 mm size fraction and the 4–8 mm and 2–4 mm size fractions for reef-flat shell-gravel (site 7) and inlet-floor mud (site 3). For encrustation, boring, and fine-scale damage, values are based on data from shell interiors; exterior-surface values are in boldface.

Size fraction (mm)	Encrustation		Boring		Fine-Scale Alteration		Edge Rounding		Fragmentation	
	4–8	2–4	4–8	2–4	4–8	2–4	4–8	2–4	4–8	2–4
Site 7 >8 mm	15% lower **25% lower**	25% lower **45% lower**	n.s. **10% lower**	40% lower **40% lower**	n.s. **10% lower**	n.s. **20% lower**	n.s.	n.s.	10% lower	n.s.
Site 3 >8 mm	n.s. **10% lower**	n.s. **15% lower**	n.s. **n.s.**	10% lower **10% lower**	n.s. **n.s.**	n.s. **n.s.**	n.s.	n.s.	15% higher	15% higher

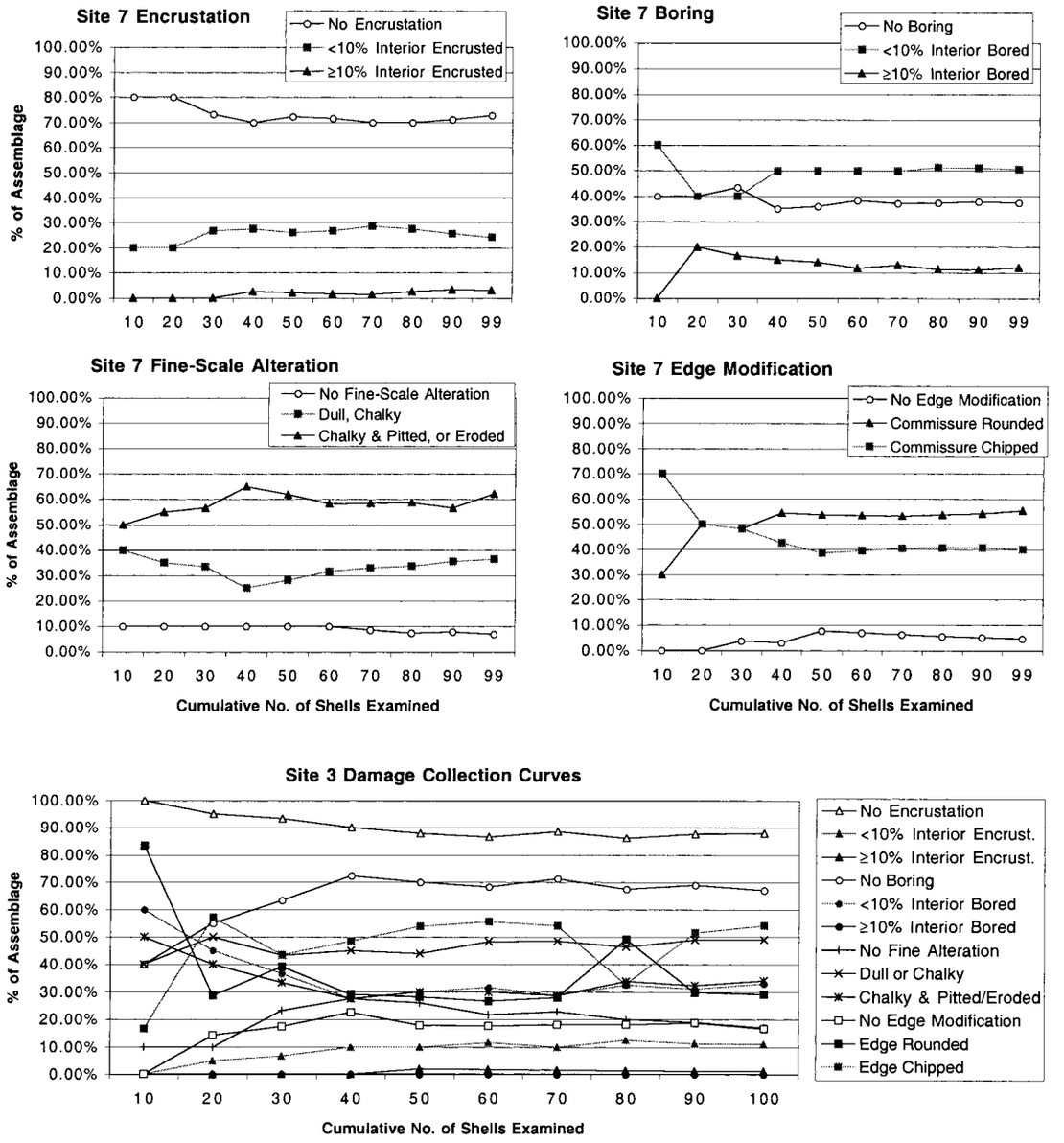

FIGURE 4—For each of the 5 taphonomic variables, damage frequency distributions are confidently stable at sample sizes of 120–150 specimens. Data for shell interiors from 2–4 mm size fractions (Fig. 3A-B).

in San Blas assemblages, among-site differences are still significant.

Exclusion of Poorly Identified Shells

Shells that only can be identified as "bivalve," rather than resolved to family or finer taxonomic level, constitute 10–20% of specimens in San Blas death assemblages. All of these specimens are fragments and exhibit significantly higher levels of damage, generally by 10 to 45 percentage points (except at site 3 mud, with low n; Fig. 7).

Thus, excluding taxonomically poorly resolved bivalve specimens lowers the damage profile of the assemblage, but the proportion of such shells in San Blas assemblages was not sufficient to affect the outcome significantly. Rank-order of variables is conserved in both subsets of the assemblage, as are among-environment trends in damage levels.

Analysis of Infaunal Shells Only

When all data from the study are considered (i.e., shells from all sites and size fractions are pooled), epifaunal shells exhibit significantly higher frequencies of all kinds of damage except fragmentation, relative to infauna. This difference persists even if only aragonitic epifauna are

TABLE 5—Contingency data for damage to interior versus exterior shell surfaces, for total data (all sites, all size fractions). Most specimens show identical levels of damage to both surfaces (boldface diagonal cells in each matrix), but, when damage is unequal, it is in most cases heaviest on the exterior surface (numbers in upper right halves of each matrix).

	Exterior Surface Damage		
	0	1	2
Encrustation Interior:			
0	**757**	538	78
1	130	**768**	341
2	6	91	**351**
Boring Interior:			
0	**550**	176	5
1	154	**1015**	238
2	1	130	**791**
Fine-Scale Alteration Interior:			
0	**49**	130	2
1	6	**924**	186
2		119	**1643**

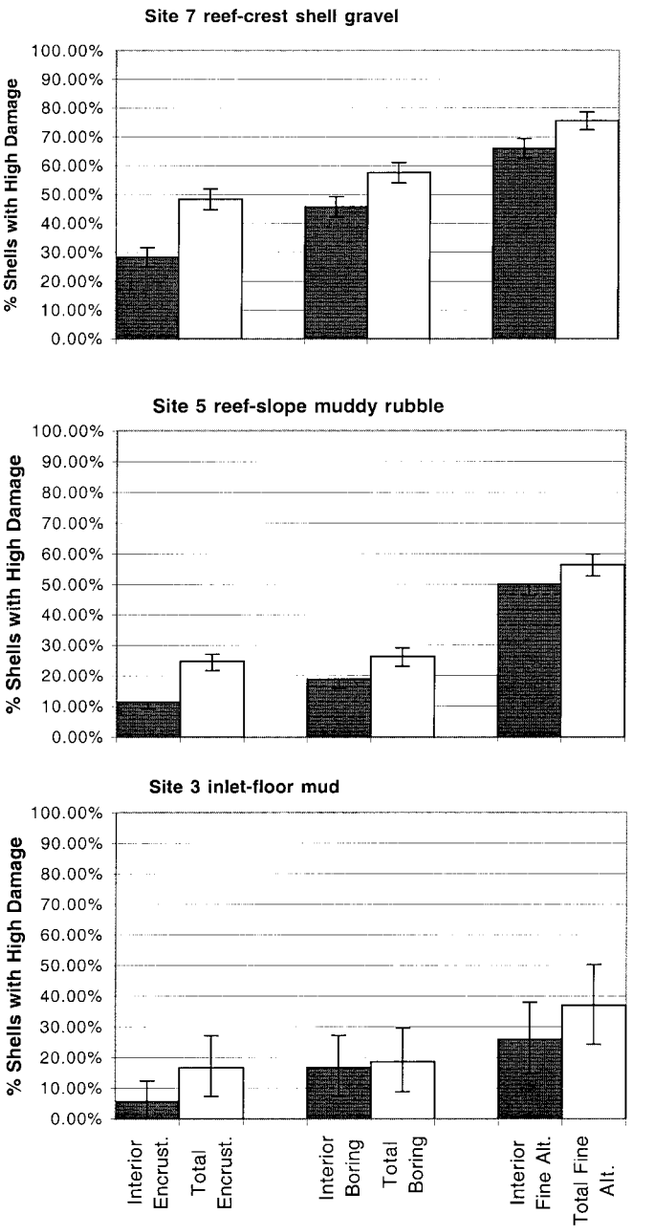

FIGURE 5—For bivalve shells >8 mm at all sites, the frequency of damage to the total surface area (white bars) is consistently higher than that scored for shell interiors only (dark bars) for each of the three relevant taphonomic variables (encrustation, boring, fine-scale alteration), and these differences are significant at all sites except site 3 mud (low n; 95% binomial C.I.).

considered (chamids, arcids, some anadarids; Fig. 8) and, thus, is linked to life-habit rather than to shell mineralogy.

Because total death assemblages include not only epifauna but also specimens that cannot be classed confidently (mostly high-damage fragments), damage assessments based on infauna-only should yield lower damage profiles than the total assemblage, and this is true in San Blas environments. At sites where epifauna constitute 50% or more of specimens in the death assemblage (site 7 reef-flat shell gravel, site 5 reef-slope muddy rubble, site 13 back-reef muddy skeletal sand), infauna-only profiles are significantly lower for 2 to 3 taphonomic variables (encrustation, boring, and fine-scale alteration; Fig. 9). Because this effect occurs at all sites, among-environment trends in damage levels are conserved.

Restriction of Data to Single Target Taxa

Of the total available assemblage, species of the infaunal bivalves *Laevicardium* and *Pitar* and of epifaunal scallops (especially *Chlamys*) were sufficiently abundant across multiple habitats to test for taxon-specific damage profiles in sites 7 (reef-flat shell gravel) and 3 (inlet-floor mud), using specimens from all size classes down to 2 mm (Appendix). Each of these target taxa exhibits higher frequencies for most variables at site 7 than at site 3, consistent with the total death assemblage (compare Fig. 10 to 2 mm sieve data in Fig. 3C-D). *Laevicardium* is most sensitive to extrinsic environment, differing in all 5 variables between the two sites, whereas *Pitar* and *Chlamys* differ significantly in only 2 variables (encrustation and boring; the total death assemblage >2 mm differs in 4 variables). *Laevicardium* also shows a strong offset in damage-levels between the two environments, comparable to the sensitivity of the total death assemblages; among-environment differences in the other two target-taxon profiles are muted. *Laevicardium* constitutes 19% of specimens in the site 3 assemblage and 13% at site 7; thus, it does not approximate total-assemblage damage simply because of numerical dominance. The proportional abundance of the other taxa are 18 and 7% for *Pitar,* and 20 and 20% for *Chlamys* (see Appendix for complete assemblage composition).

The damage profiles of the three taxa differ significantly from each other within each site, both in frequency of damage and in rank-order of variables (Fig. 10), showing

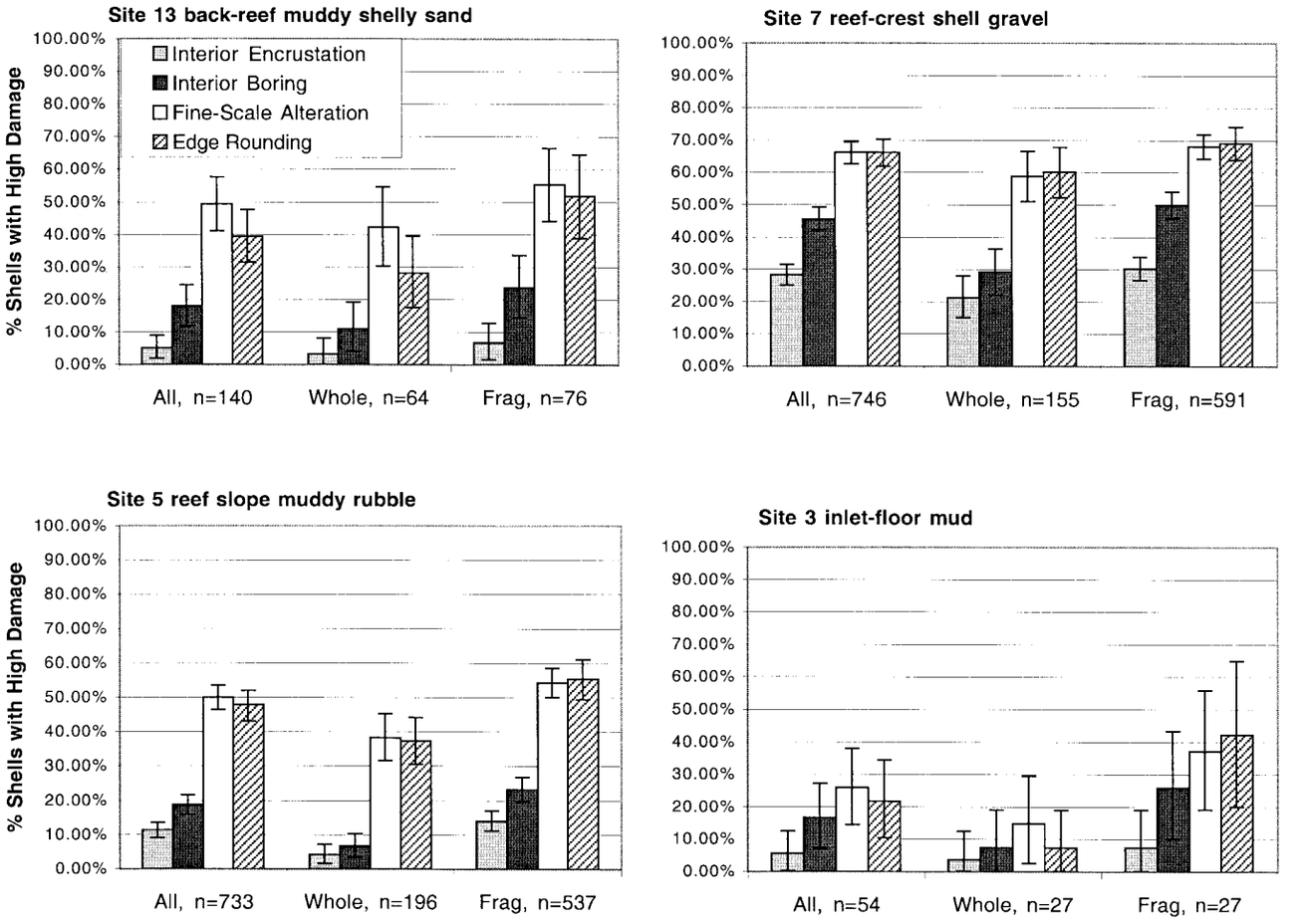

FIGURE 6—Fragments consistently yield significantly higher frequencies of damage (interior surfaces) than whole shells in the same > 8 mm size fraction, in all environments tested. 95% binomial C.I.s.

the effect of intrinsic, taxon-specific factors on shell condition. Some of these differences are understandable in terms of shell morphology. For example at site 7, *Chlamys* exhibits less edge-rounding than the others probably because of its exceptionally thin commissure, which is either less prone to rounding (versus chipping) or less easy to recognize as rounded under 10× magnification; at both sites 7 and 3, *Pitar* exhibits less fragmentation than *Laevicardium*, probably because most *Pitar* specimens are small [2–4 mm fraction, versus >8 mm for *Laevicardium*, and fragmentation is elevated in fine size fractions in general (see earlier section)]. Explanations for other differences are more obscure (e.g., *Pitar*'s higher fine-scale alteration and rounding than *Laevicardium*, despite the same general microstructure and thinner commissures).

Of the three taxa, *Laevicardium* damage provides the best match in level and rank-order to the profile of the total death assemblage in both site 7 and 3 (Fig. 10 versus 2 mm sieve data in Fig. 3C-D). *Laevicardium* profiles also agree well with the total-infaunal damage profiles (Fig. 10). It is not clear, however, why this particular taxon provides the closest proxy to more inclusive datasets, because *Laevicardium* dominates neither the total death assemblage nor the infaunal component of either site (Appendix). A second cardiid genus, *Americardium*, occurs in sufficient abundance at site 7 to evaluate, but on all variables, damage to this coarsely ribbed quadrate bivalve differs significantly from *Laevicardium* (large, smooth-surfaced egg-shape), and matches *Pitar* (small, smooth-surfaced venerid) on all variables except fragmentation.

Other Forms of Data and Methods of Analysis

Data on damage to individual shells can be gathered and manipulated in several ways. Key choices in data-gathering include whether taphonomic variables are treated (1) as a set of linked conditions, that is multi-factorial grades *sensu* Flessa et al. (1993; Meldahl et al., 1997a), or (2) independently (e.g., encrustation versus boring, etc.), as in this and most other studies (Table 1). Key choices in handling data on damage states include whether (a) the full frequency distribution is analyzed (stacked bar-graphs of Feige and Fürsich, 1991; ternary taphograms of Kowalewski et al., 1994, 1995), or (b) the information is reduced to, for example, the frequency of high-intensity damage (as here; % shells in the highest category

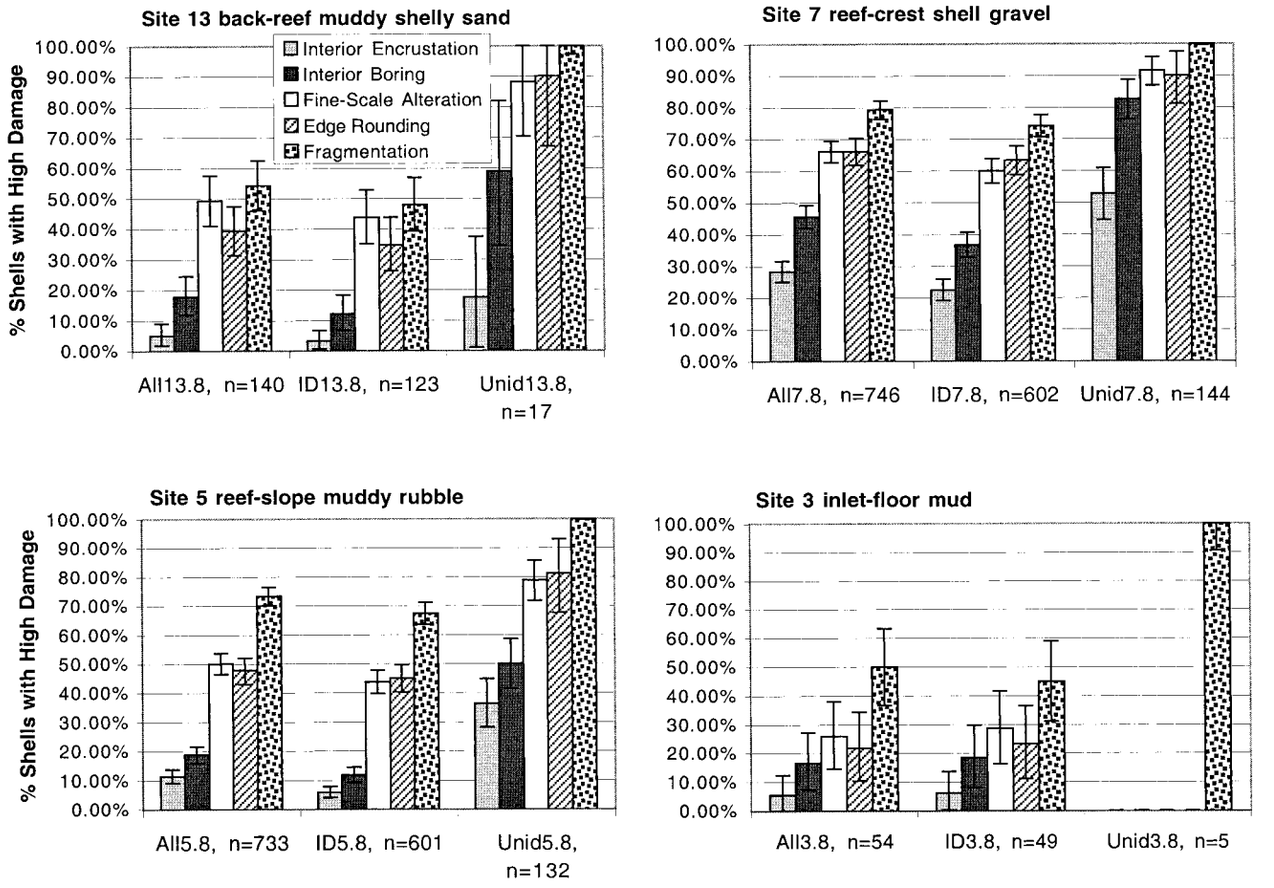

FIGURE 7—Shells that can be classed only as bivalve in origin (bars labelled ''unid'') consistently yield significantly higher frequencies of damage than specimens that can be identified to species, genus, or family level (bars labelled ''ID''); >8 mm size fraction, interior damage only; 95% binomial C.I.s. ''All'' denotes total sample.

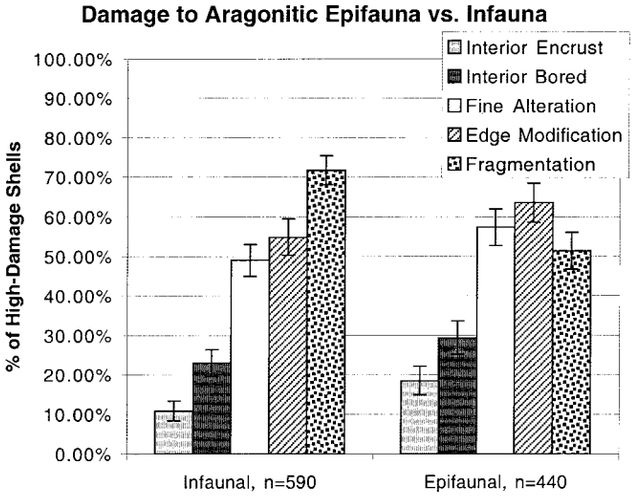

FIGURE 8—Based on analysis of the total San Blas dataset (all sites, all size fractions), shells of epifaunal bivalves exhibit significantly higher frequencies of all kinds of damage except fragmentation than infaunal shells, even if (as here) epifauna are limited to those with aragonitic shells.

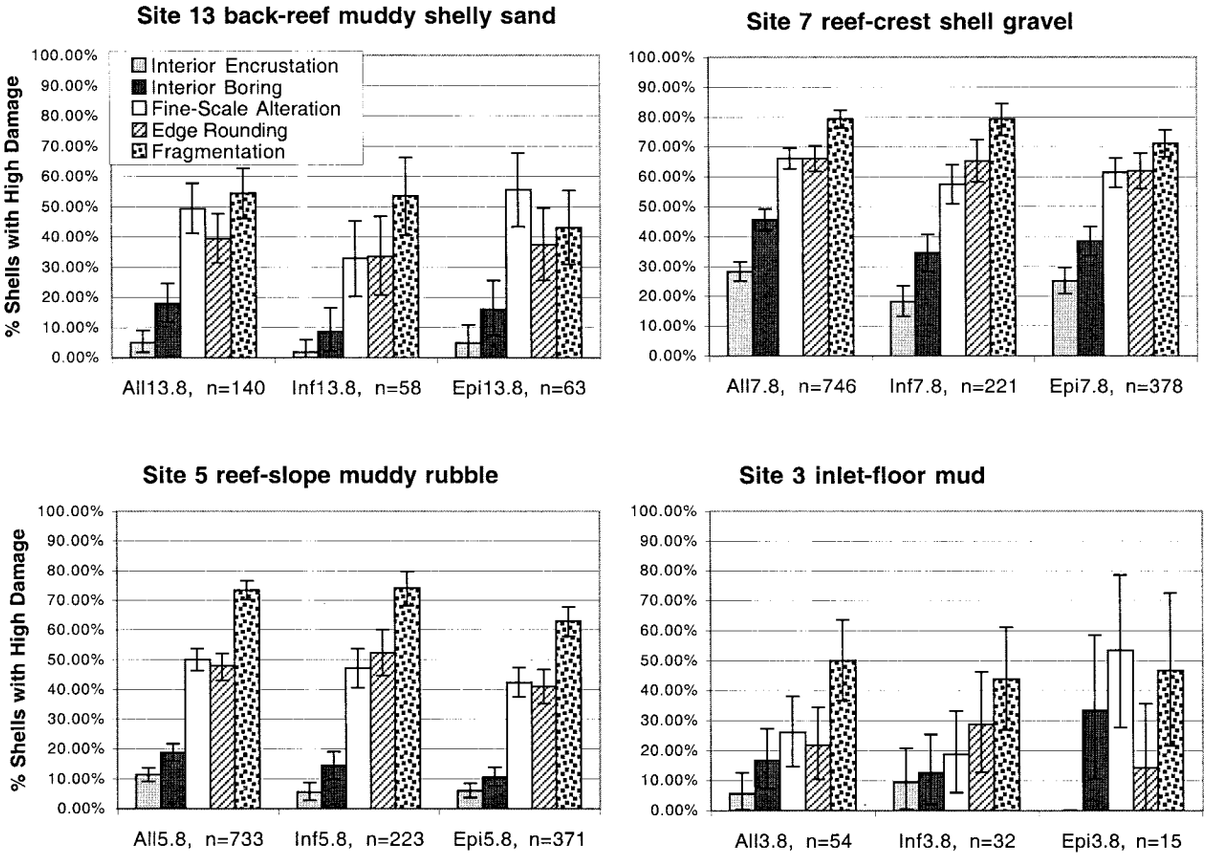

FIGURE 9—Damage profiles generated by infaunal shells only (bars labelled ''Inf'') are lower than total-assemblage profiles (''All''), which include epifaunal specimens (''Epi'') and specimens that cannot be classed to life-habit (mostly highly damaged fragments). Data are for >8 mm size fractions, interior-surfaces only; 95% binomial C.I.s.

on the damage scale), presence-absence (% shells having any degree of damage), or average damage state (mean degree of damage: Parsons, 1993; Meldahl et al., 1997a).

Figure 11 presents the full frequency distribution of damage states in the >8 mm size fraction (interior damage only) as stacked bar graphs. (The baseline high-intensity damage profile of Fig. 2 uses only the black segments of these bars.) Although confidence intervals for San Blas datasets are sufficiently small that they do not overlap among bar-segments, this could be a complicating problem

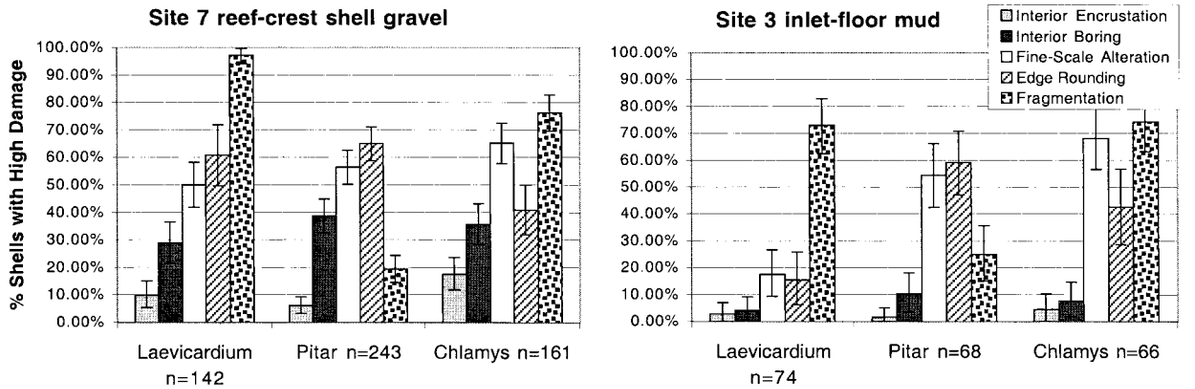

FIGURE 10—Damage profiles for >2 mm specimens of the infaunal bivalves *Laevicardium* and *Pitar,* and the epifaunal scallop *Chlamys* at sites 7 and 3 (multiple species of each genus; Appendix). Each target taxon detects a decrease in damage-levels from site 7 to site 3, but differ significantly from one another within each site in level of damage and rank-order of variables. *Laevicardium* provides the closest match to the damage profile of the total death assemblage (>2 mm data in Fig. 3C-D).

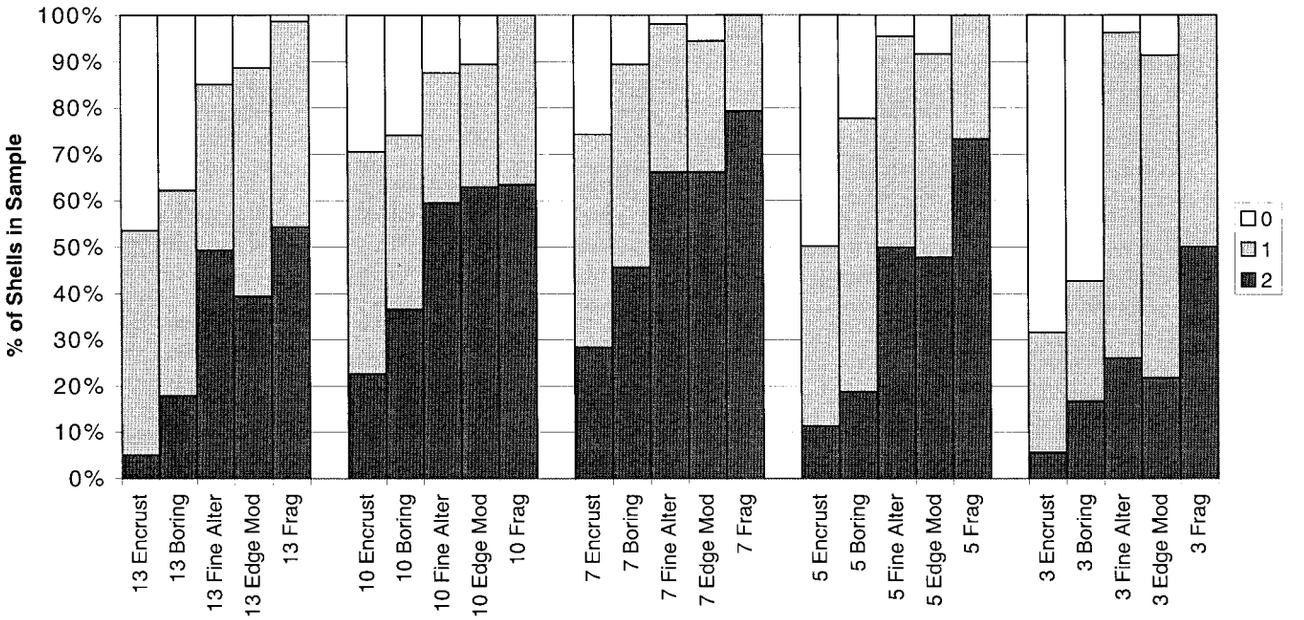

FIGURE 11—Stacked-bar graphs displaying the full frequency distribution of damage states (0–2, defined in Table 2) for taphonomic variables in >8 mm size fractions (interior damage only). The black segments of bars indicate the frequency of high-damage states (2), and are the basis of the baseline damage profiles of Figure 2. 95% binomial C.I.s. Encrust = encrustation; Fine Alter = fine-scale surface alteration; Edge Mod = edge modification (edge-rounding is state 2); Frag = fragmentation.

in datasets with smaller sample sizes. Stacked bar-graphs like these are effective in revealing similarities among sites in rank-order of variables as well as significant differences on a variable-by-variable basis, and any number of states per variable can be accommodated.

Because degrees of damage in San Blas assemblages are categorized into three states (bins) per variable, these data also can be plotted on ternary diagrams (Fig. 12A-E). Taphograms are very effective in depicting the end-member nature of the reef-flat shell gravel and the inlet-floor mud, the specific natures of these assemblages, and, with the addition of 95% confidence intervals, the significance of among-site differences. For all variables except fragmentation, (a) replicate reef-flat shell gravel sites 7 and 10 plot as nearest neighbors to each other and also closest to the "high damage" pole, (b) inlet-floor mud site 3 plots maximally distant from these shell-gravel and closest to the "no damage" pole, and (c) muddy shell sites 5 and 13 plot in intermediate positions and quite close to one another on most variables. These taphograms also are effective in demonstrating that even when sites are very similar or not significantly different in some kinds of high-intensity damage, they may still separate on the basis of pristine (no-damage) shells (e.g., sites 3, 5, and 13 with respect to boring).

When all variables for all sites are plotted on a single taphogram (Fig. 12F), the end-member sites (7 and 10, versus 3) occupy non-overlapping areas, again demonstrating the utility of taphograms in distinguishing samples. This plot highlights a disadvantage of taphograms, however, in that similarities among sites in the rank order of variables are hidden completely, in contrast to the stacked bar graphs and high-intensity damage profiles. Another disadvantage is that degrees of damage must be categorized into (or otherwise collapsed into) 3 states per variable (see examples in Kowalewski et al., 1995).

In Figure 13A-B, taphograms of encrustation and boring data are used to display the effect of using different size fractions of an assemblage (points within clouds) and of gathering data from total shell surfaces rather than from interior surfaces only (points connected by arrows). On taphograms, 2–4 mm size fractions plot significantly closer to the "good" (i.e., pristine, no damage) corner than their counterpart 4–8 mm and >8 mm fractions for the same site, and the magnitude of the effect for encrustation and boring is sufficient to move points into different sectors of the diagram (data for sites 3 and 7 only; Fig. 13A-B). When data for the >8 mm faction is based on total shell surface rather than interiors only, the value for each site shifts significantly toward a higher-damage corner but generally stays within the same sector of the taphogram (Fig. 13A-B). Clouds drawn around sets of points reflect the size of the combined 95% confidence limits for points from that site.

The divergence of damage levels on target taxa from each other and from damage to the total-assemblage (discussed in previous section) is clarified by plotting on ternary taphograms (Fig. 13C-F). Five patterns are evident.

(1) *Laevicardium* is the only taxon that consistently retains the two end-member sites in their correct relative positions for all five variables; that is, placing site 3 significantly closer to a lower-damage corner than site 7. *Chlamys* and *Pitar* each capture these relative positions based on encrustation and boring levels, but scramble the site

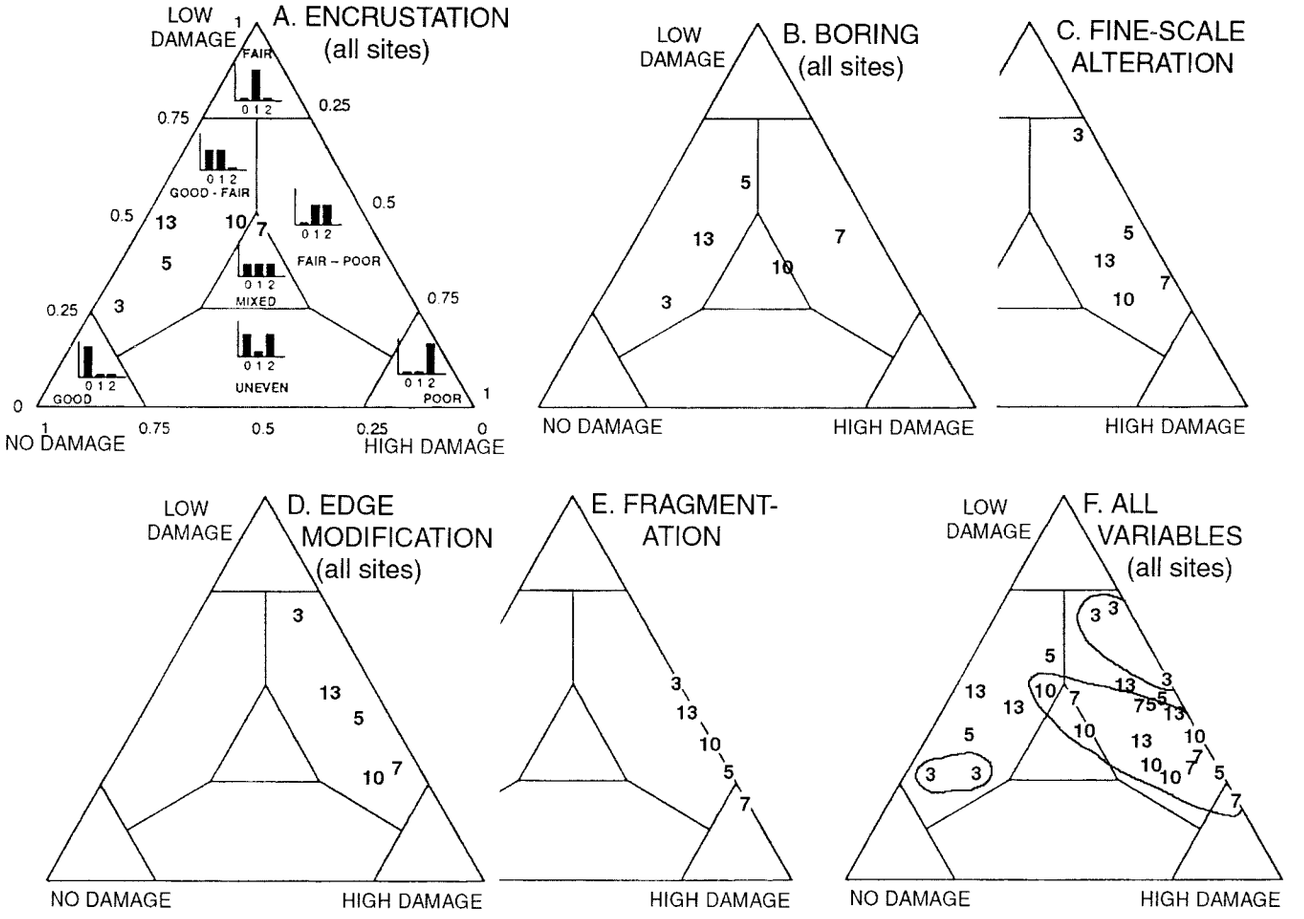

FIGURE 12—Data from Figure 11 replotted on ternary taphogram template of Kowalewski et al. (1995; see other figures for confidence intervals). Taphograms A-E plot the relative frequencies of damage states in each site for single variables. Taphogram F plots data for all variables and all sites on a single diagram, underscoring the end-member nature of damage levels in reef-flat shell gravel sites 7 and 10, and inlet-floor mud site 3, which form non-overlapping clouds of points. These diagrams are possible only because degrees of damage were categorized into three states (bins) per variable (Fig. 11, Table 2).

positions or show no significant difference between the two sites when scored for other kinds of damage.

(2) *Laevicardium* nonetheless is offset significantly from total-assemblage values for some variables, and no target taxon does better than the others at matching total assemblage damage (2 mm sieve data) for all variables. This is contrary to the finding using high-intensity damage, where *Laevicardium* was a close match to the 2 mm-sieve total-assemblage data (earlier section; Figs. 10 and 3C-D).

(3) Target taxa display relatively high disparity for all variables at site 3 compared to their behavior at site 7 (compare clouds of points). Fragmentation is the only exceptional variable, with high disparity among taxa at both sites.

(4) For all variables, site-3 *Chlamys* shells plot as close or closer to site-7 *Chlamys* than to other site-3 target taxa or to the total-assemblage value at site-3, suggesting either a strong intrinsic control on damage levels (i.e., similar signature regardless of post-mortem environment) or import of specimens from site 7, where they acquired their signature. Consideration of the high-intensity damage profile (Fig. 10), showing the same basic profile for *Chlamys* at both sites but simply higher frequencies of damage, argue that intrinsic effects rather than post-mortem transport are most important. Site-3 *Pitar* specimens lie as close or closer to site-7 *Pitar* than to other site-3 values for only three variables (fine-scale alteration, edge modification, and fragmentation), whereas *Laevicardium* damage levels at the two sites are quite different and closer to the value for the total-assemblage from which they are drawn. Thus, intrinsic factors are moderately important for *Pitar*, and least important for *Laevicardium*, whose damage levels in the two sites are quite different from each other and closer to the value for the total-assemblage from which they are drawn.

(5) Consistent with analysis of the total assemblage (Figs. 8 and 9), the epifaunal bivalve *Chlamys* plots closer to a higher-damage corner than the other two (infaunal) target taxa for 3 of the 5 taphonomic variables.

Because most shells exhibit some degree of fine-scale alteration, edge modification, and disarticulation/fragmentation, presence-absence information is less effective than

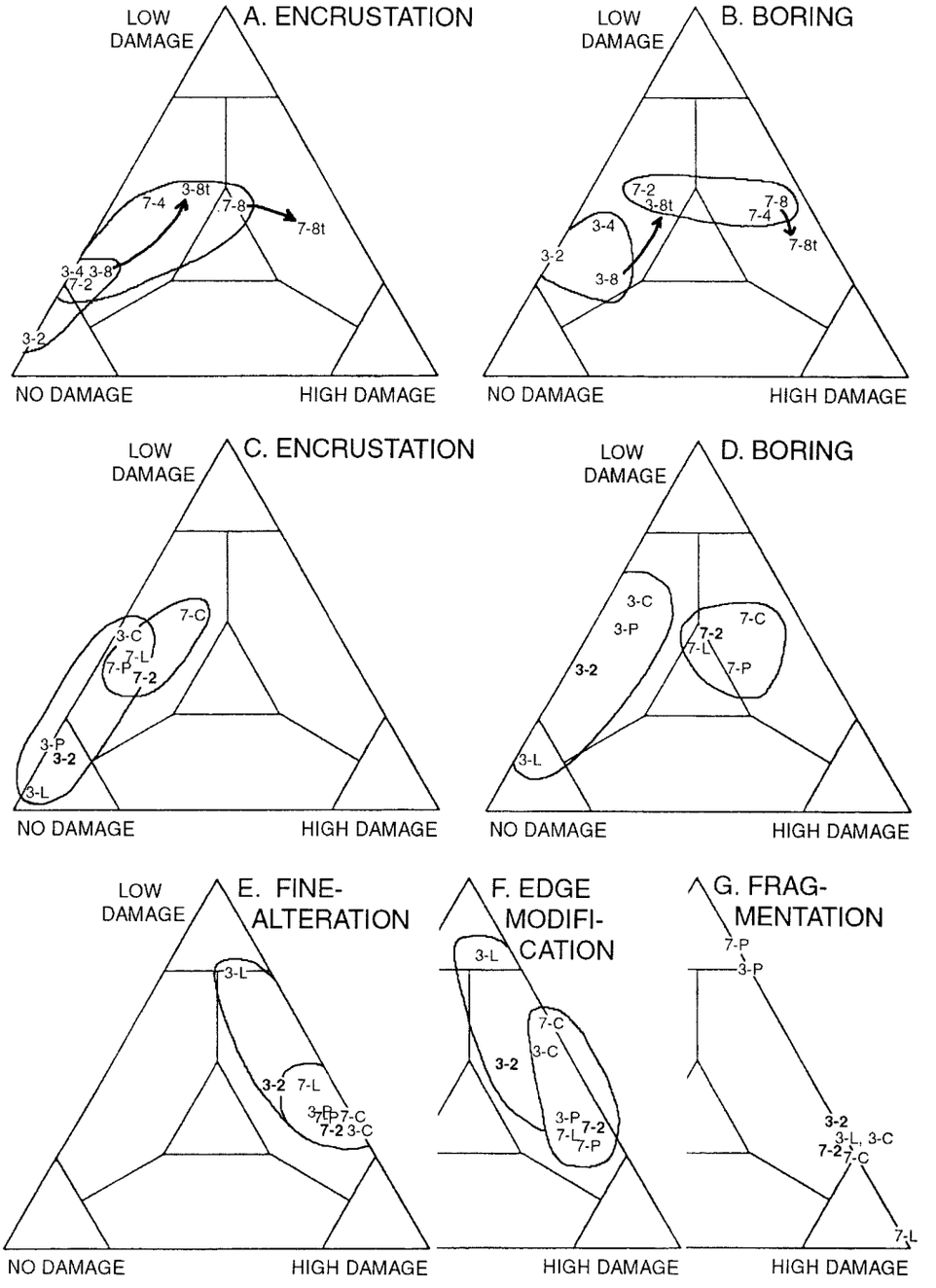

FIGURE 13—Effect of size-fraction, total surface area, and target taxa on full-frequency data, displayed using taphograms. Clouds drawn around sets of points for a site reflect the size of the combined 95% confidence intervals for those points. (A and B): At end-member sites 3 and 7, damage levels for the fine size-fraction (2–4 mm) plot in lower-damage portions of taphograms than counterpart 4–8 mm and >8 mm fractions, with the effect most pronounced for boring and encrustation (note position within clouds). Data points for size-fractions denoted, respectively, by −2, −4, and −8 attached to site number; damage to interior surface only. Scoring damage to total shell surface area (symbol "t") rather than interior-only shifts values toward a higher-damage portion of taphogram (>8 mm size fraction; arrow). (C-F): Damage levels for target genera *Laevicardium* (-L), *Pitar* (-P), and *Chlamys* (-C) plot at varied distances from total- assemblage values (based on all >2 mm specimens; interior damage only; boldface site numbers with −2 suffix). *Laevicardium* is the only target that captures the relative positioning of total-assemblage damage on the plots, with site 3 specimens closer to low-damage corners than site 7 specimens, but is not a consistent proxy for (nearest-neighbor to) total-assemblage damage values. Site-3 *Chlamys* plots closer to site-7 *Chlamys* than to other site-3 target taxa or total-assemblage values, indicating intrinsic control of damage patterns in this epifaunal genus or possible import from site 7.

high-intensity damage and full-frequency distribution data in discriminating the San Blas samples (presence-absence data combines the shaded high-damage and moderate-damage segments of bars in Fig. 11). Most pairwise comparisons of sites differ significantly in only two variables at most (most commonly boring and encrustation), including end-member sites 3 and 7. The lack of resolving power of presence-absence data is underscored visually in a line-plot of the same data (Fig. 14B). Compared with high-intensity frequency data (plotted in line-graph form in Fig. 14A), which shows damage of all types increasing across the transect to maximum values in reef-flat shell-gravel sites 7 and 10, only two of the variables exhibit such trends in presence-absence data.

"Average damage state" (calculated from the data in Fig. 11) shows intermediate power to discriminate environmental differences in damage frequency to high-intensity and presence-absence data, as shown in the line-graph of Figure 14C. The rank-order of variables is the same as for high-intensity data (Fig. 14A), but this would not necessarily occur if the variables differed in numbers of states—that is, if some variables had 2 or 4 or 5 states, instead of all having 3.

Use of Multiple Evaluators

All data used in this study were collected by a single operator (TAR). However, to estimate operator error, two of us (one trained by the other) independently collected data from the same sample (two small samples from site 3, >8 mm fraction, n = 44). The two operators showed high agreement in assessing the frequency of high degrees of damage in the assemblage, but differed significantly in parsing shells among categories of low and no damage. In fact, differences were sufficient for the same assemblage to plot in different sectors in ternary taphograms, where these full-frequency data are employed. On the positive side, the operators were consistent in either under- or over-scoring the pristine (no-damage) category relative to the other; hence, a compensation factor could have been calculated.

These results suggest that (a) not surprisingly, data collected by a single operator will be superior to that pooled from multiple operators, but (b) if multiple operators are necessary, the most reliable data may be those based on scoring a single, high threshold of damage, rather than the frequency distribution of all damage states for a variable. The larger the number of states per variable, the larger the likely error among operators because of subjectivity in estimation. Thus, it is worth stressing the obvious that, when using multiple operators, double-blind tests of consistency are essential.

DISCUSSION

The results of these sensitivity tests, and their implications for taphofacies analysis, are summarized in Table 6. Of the variables tested, sample size has received little explicit attention for its effect on taphonomic signatures. Based on the present analysis, samples smaller than 20 specimens (whether single sample or set of pooled samples) are insufficient to determine taphonomic signatures for multi-species assemblages, especially given the

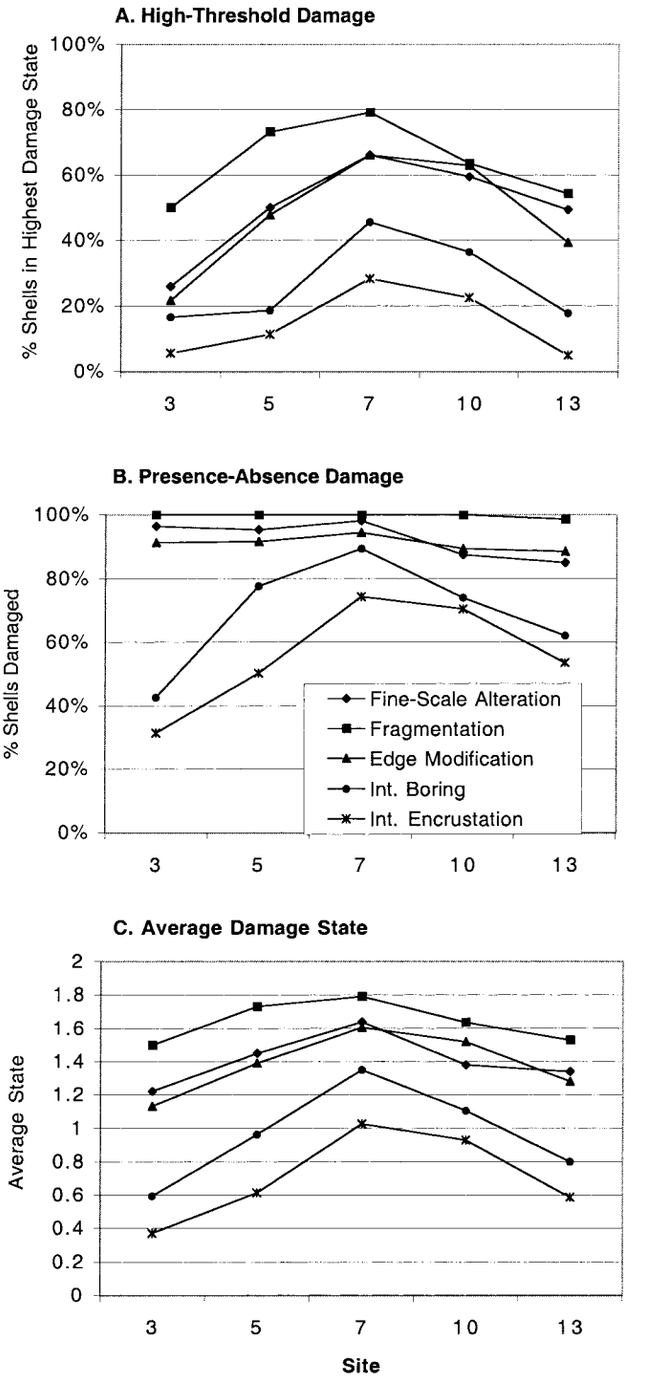

FIGURE 14—Sensitivity of between-site differences in damage levels and rank-order of variables as a function of damage metric, plotted as line-graphs (>8 mm size fraction, interior damage only). (A) Frequency of high-intensity damage (same data as Fig. 2, and black segments of bars in Fig. 11). (B) Presence-absence data (combined shaded segments of bars in Fig. 11); note that only 2 variables differ in value among sites; rank-orders of variables are preserved; fragmentation here is disarticulation (see Table 2). (C) Average damage state (calculated from full bars in Fig. 11; 0 = no damage, 1 = low damage, 2 = high damage from Table 2); muted ability from high-intensity damage to differentiate levels of damage at sites, but generates the same rank-ordering of variables and detects similarity in those orders among sites.

TABLE 6—Summary of test results.

Test	Results (for high-intensity damage)	Caveats & Implications
Sieve size	Lower frequencies of damage (except fragmentation) in finer size fractions (<4 mm), but basic shape of damage profile and between-environment differences are maintained	Measured damage levels will be lower in studies using finer sieves, due to numerical dominance of small specimens
Sample size	120–150 specimens necessary for profile to stabilize in multi-species assemblages	50 shells will give rudimentary information, but statistical power is low
Damage to total shell vs. shell interior only	Shell exteriors sustain equivalent or greater damage, but basic shape of damage profile and between-environment differences are maintained	Effect is strongest in coarsest grained environments; damage levels based on total shell surface will be inflated relative to those on interiors-only
Exclusion of fragments	Fragments exhibit higher frequencies of all damage types, but same rank-order of variables as whole shells	Depending on frequency of fragmentation, damage profile of assemblage is lowered if score whole shells only
Exclusion of taxonomically poorly resolved specimens	All such specimens are fragments, with higher frequencies of damage than shells that can be identified to family, genus, or species	Depending on frequency of such specimens, damage profile of assemblage is lowered if score well-resolved specimens only
Focus on infaunal species	Infaunal shells exhibit lower frequencies of damage than epifauna, even when mineralogy is held constant (aragonitic taxa only)	Infauna-only profiles are lower than total-assemblage profiles, but between-environment trends are conserved
Focus on damage to single taxa	Individual taxa detect environmental differences in damage-levels, but only one of three taxa tested is as effective as the total death assemblage	Taxa can yield disparate rank-ordering of variables; intrinsic controls on shell damage reduce the utility of single taxa as proxies of total-assemblage damage
Other metrics of assemblage condition	Presence-absence data least effective and average damage-state intermediate power to distinguish sites	Ternary taphograms make effective use of full-frequency data, but provide no rank-order insight on variables in signature
Operator error	Consistent results in recognizing high-damage states of variables, but significant variance for zero and low-damage states	If multiple operators to be employed, data on high-intensity damage may be most robust

among-taxa heterogeneity in signature evident from our target-taxa analysis (above). At the other extreme, 20,000 specimens are almost certainly overkill; this range is encompassed by studies in Table 1. The 20–30 specimens rule-of-thumb used by many may be sufficient for taphonomic characterization of single target taxa. However, the best overall strategy is to generate collection curves to establish, using material at hand, when an adequate number of specimens has been examined and data collection can reasonably stop, rather than targeting *a piori* a particular number of specimens or volume of sediment. From the suite of San Blas habitats, minimum necessary sample sizes were on the order of 50–100 specimens, depending on the homogeneity of damage and the number of taphonomic variables. Based on rarefaction analysis of other samples from the Bocas del Toro and San Blas areas of Panama, Best (1998; 2000) found that sample sizes of 200 specimens are necessary when a fuller array of taphonomic states (not collapsed to 3 per variable), an additional variable (alteration color), and the taxonomic composition of borers and encrusters are to be quantified.

Differences in damage levels among size fractions and between whole shells and fragments have been examined in molluscan death assemblages by a number of workers. Staff and Powell (1990) used a protocol very similar to the one used here for mollusk assemblages from the Texas continental shelf (silty siliciclastic sands) and came to similar results: fragmentation is higher in the fine fraction (4–12 mm), but "biotic interactions" (encrustation and boring, including predatory drillholes) are higher among large shells (>12 mm, 2 of 3 sample sites); and fragments and whole specimens have similar overall signatures, but fragments—especially "minor fragments" lacking hinges or whorl apices—exhibit much greater "dissolution" (fine-scale alteration of all types) and edge rounding. In continental slope cold-seep assemblages, Callender and Powell (1992; Callender et al., 1992) also found higher damage among fragments from "dissolution" and rounding, but whole shells had higher frequencies of "biotic interactions." The same patterns pertain in higher-energy and/or coarser-grained settings: higher levels of damage among larger shells (e.g., from borings by Boekschoten, 1966; of all damage types for bivalve shells >2 cm by Bosence, 1979; from "dissolution" by Davies et al., 1989), and higher damage levels among fragments than among whole shells (e.g., edge-rounding and surface abrasion by Davies et al., 1989; and see Pilkey, 1964, and Pilkey et al., 1969, on same pattern in palimpsest shelf sands).

Studies of the effect of unidentifiable specimens consistently find that their inclusion increases the documented damage level for a sample (qualitative statement in Davies et al., 1989; data in Staff and Powell, 1990, and Callender et al., 1992; this study, Fig. 7). Davies et al. (1989) and Staff and Powell (1990) recommended including "unidentifiable" material for its greater sensitivity to detailed environmental differences. In contrast, "unidentifiable" material (all fragments) in the present study was not found to have greater sensitivity than identifiable materi-

al: damage levels were higher in all environments, but among-environment differences were proportional to those for identifiable material. As a caveat, because operators will differ in the cut-off they use between identifiable and unidentifiable material (if the protocol is to ignore unidentifiable material), and because operators also will differ in their skill in identifying "unidentifiable" shells as molluscan (that is, how far down into "debris" they will venture), unidentifiable material creates a certain degree of subjectivity in taphofacies analysis regardless of protocol. That is, the more exclusionary the operator, the lower the damage profile. Individual operators should achieve consistency within a study, but cross-study comparisons will be less secure. Thus, the key caveat in cross-study comparisons will be to treat studies that include unidentifiable fragments separately from those that use only identifiable fragments, and to partition both of these from studies that use only whole shells.

The effect of focusing on only infaunal or epifaunal specimens has been evaluated in few studies, but these consistently find higher damage among epifaunal specimens (as found herein; Figs. 8 and 9; and see plots of epifaunal *Chlamys* compared to the two infaunal target taxa in Fig. 13). Using the same protocol for samples from Bocas del Toro, Panama, Best and Kidwell (2000b) found higher damage levels among epifaunal shells (interior surface only) in both soft-sediment and hard-substratum environments. Parsons (1993; Parsons and Brett, 1991) cited higher damage levels in epifaunal than infaunal subsets of reefal samples from the Virgin Islands (insufficient epifauna to test in soft-sediment settings); this included damage to shell exteriors that was recognized as potentially being ecological rather than post-mortem in origin. Dent (1995) also reported higher levels of encrustation and boring for two epifaunal target taxa than for an infaunal taxon in a range of carbonate environments of southern Florida (also includes damage to exterior shell surfaces).

One of the most interesting and tantalizing results is the effect of individual "target" taxa on perceived damage levels. As reviewed by Best and Kidwell (2000b), individual taxa typically yield different levels of damage—and in some instances different rank-orders of variables, or trends along environmental gradients—from the source assemblage as a whole and from other target taxa, even when those taxa are of the same life-habit or mineralogy (e.g., Feige and Fürsich, 1991; Dent, 1995). Staff and Powell (1990) found that their target taxa (delicate infaunal bivalves *Abra* and *Tellina*) bore very similar signatures to each other, differing only in the percentage that retained periostracum and the degree of edge modification; these taxa strongly resembled the source assemblage (perhaps because they jointly dominate it, constituting 41% and 23% of the assemblage, respectively; ditto target taxa in Callender and Powell, 1992). Thus, the results of the present study are consistent with previous studies in recognizing high inter-genus variability in taphonomic signature. In the present study, disparity among target taxa is greater in the fine-grained facies than in the shell-gravel facies (site 3 versus site 7 in Fig. 13C-G), and the magnitude of this effect on signature is comparable to that of size-fraction (compare with clouds of points for same sites in Fig. 13A-B). Consequently, although target taxa are an extremely valuable approach for some purposes (e.g., calibrating taphonomic clocks among environments; Meldahl et al., 1997a), their use as a substitute for or as an indicator of overall assemblage condition in paleoenvironmental analysis requires caution. The raw data in the Appendix underscore another, secondary effect of the choice of sieve size on taphonomic signature, and that is variation in taxonomic composition among size fractions, an effect well known to benthic ecologists (Reish, 1959; Bachelet, 1990). To the extent that taxonomic composition influences taphonomic signature, then sieve-size will influence which part of that signature is captured or weighted; this effect is in addition to the differential attractiveness of large and small specimens to colonizing infestors.

Other studies find that damage to exterior surfaces of shells are generally as great or greater than damage to interior surfaces, based on measures of "dissolution" and/or abrasion (i.e., fine-scale alteration; Davies et al., 1989; Staff and Powell, 1990; Callender et al., 1992; Kowalewski et al., 1995). These results are consistent with the present investigation. Additionally, there is significantly higher damage from encrustation and boring to shell exteriors, which has not been tested in previous studies ("biotic interactions" negligible in frequency, or damage scored only for total surface area).

Ternary taphograms are extremely effective graphically in capturing differences and similarities in full-frequency data, but it is cumbersome to include the confidence intervals that would permit the dispersion of points to be evaluated statistically. Although they use only part of the frequency data, threshold damage profiles (e.g., Fig. 2; or line-graph variants of these—Fig. 14A) are most effective in evaluating, both statistically and visually, the qualitative aspects of these taphonomic signatures, namely the rank-order importance of variables. Thus, these are a valuable and arguably essential complement to taphograms. These require no additional data to be collected, only a regraphing of a subset of data, and the admittedly higher space–demand relative to points on a ternary taphogram (Kowalewski et al., 1994) can be reduced by plotting only one damage-profile per facies (pooled set of samples; e.g., Best and Kidwell, 2000a), rather than one per sample as here. Rank-order insights are otherwise difficult to extract from sets of univariate taphograms (e.g., Fig. 12), from average-state data (which suppress among-site differences), and from pairwise and multiple analyses of variance (e.g., tables as in Staff and Powell, 1990), and, as a result, the "overall signature" of a death assemblage is down-played.

In these San Blas samples, high-intensity damage was the most useful threshold for plotting damage profiles because the contrast between reef and mud assemblages in damage intensity was so great. Notice from the full-frequency data in Figure 11, however, that to distinguish among fine-grained sites, a lower threshold would be equally or more effective (e.g., state 1 rather than state 2 damage for sites 13, 5, and 3). Other muddy assemblages from the San Blas Archipelago (Best, 2000) and from Bocas del Toro (Best and Kidwell, 2000a), for example, have lower intensities of boring and especially encrustation, as do assemblages from temperate subtidal mud (e.g., negligible "biotic interactions" on shells from continental shelf and slope sites summarized in Callender et al., 1992), and their signatures might be indistinguishable were only

high-intensity damage to be plotted. The taphonomic signatures of sites 13 and 5 almost certainly are influenced to some degree by reef-derived skeletal material, introduced either via transport or via faunal condensation from habitat-patch migration over the period of time-averaging, given the proximity of these sites to the reef. Across this "mini-transect," environments constitute a continuum of taphonomic processes and ecological inputs: it is impressive that taphofacies analysis distinguishes these sites as well as it does, as some might be lumped in other settings, and signatures are, in fact, less distinct than those of more disparate environments sampled in the larger San Blas Archipelago (Best, 2000; and compare with Bocas del Toro, Best and Kidwell, 2000a).

Here and in most studies (Table 1), each taphonomic variable is treated independently, using a separate set of damage *states* to categorize the extent of shell modification (ordinal taphonomic grades *sensu* Kowalewski et al., 1994; see Pilkey et al., 1969, 1979, and Davies et al., 1989, for earlier variants). A number of taphofacies studies have employed a more summary form of "taphonomic grades" to evaluate individual shells (and see Brandt, 1989, for categorization of entire assemblages). By this alternative method, taphonomic data are composed of a number of qualitative categories, each describing the overall extent of modification when fragmentation, abrasion, surface alteration, bioerosion, encrusting, etc., are jointly taken into consideration. Frey and Howard (1986; Henderson and Frey, 1986) are an early example, using a specific set of features to score individual shells as "new" or "old" (2-grade system based on preservation of original color and luster, and persistence of ligament and/or periostracum); overall sample condition was characterized by the ratio of new to old valves. Flessa et al. (1993; Meldahl et al., 1997a) devised grading systems for Gulf of California mollusks based on larger arrays of variables and a more finely divided spectrum of damage (4 ordinal grades); "average grade" was used to describe overall sample condition. Each grade is characterized by a suite of taphonomic characteristics: e.g., 1 = no visible bioerosion, encrustation, or other alteration; 2 = dulling of original luster, $<$10% of bioerosion or encrustation on interior valve surface, etc.

A major advantage of collecting such "summary grade" taphonomic data is that the preservational quality of individual shells and assemblages can be assessed very quickly. If researchers use a single, common grading system, this approach also would establish consistency among evaluators and facilitate cross-study comparisons (as it has been used in Gulf of California mollusk studies—Flessa et al., 1993; Meldahl et al., 1997a). Two problematic aspects of this type of data are in (1) the potential for grouping shells (and samples) that are really quite different (e.g., with one having high levels of encrustation and the other high boring but each scoring as grade 4), and (2) the potential for having, for example, bio-infestation of one grade and fine-scale alteration or abrasion of another grade on a single shell. Protocols could be established to deal with this latter situation—for example, having evaluators always score shells by the higher of the two possible grades—but this only skirts the underlying ambiguity. Fundamentally, although all variables are considered at once, this system stresses damage level and subsumes rank-order importance of variables. In addition, grades developed on the basis of suites of damage in one area may not include the range of alteration or the combinations of states that can occur in another area (for example, the disparate ranges of damage to shells in temperate soft-sediments versus those in reef assemblages); thus, broader comparisons of data may be difficult.

In San Blas samples, it was not clear, even in retrospect, that taphonomic variables co-varied as regularly—or at least in the same way—as in Gulf of California material such that this kind of grading system would be effective. Thus, this approach to analysis was not pursued. Ideally, one could conduct a multivariate analysis of pilot data (with shells scored for independent variables) to search for the most effective and locally relevant "natural" grades, thereby reducing several states/variables into single scores. This customized grading system would speed subsequent data collection. However, it is not clear that it would reduce some of the inherent ambiguities of the approach, unless the multivariate analysis proved the existence of distinct classes rather than continua in damage.

Another factor that was not pursued explicitly is the choice and number of variables considered. By inspection (data in Fig. 11), it is clear that the number (and best choice) of variables needed to differentiate facies depends on whether the metric is to be presence-absence, high-intensity, or full-frequency data. Increasing the number of variables and states per variable would increase one's ability to differentiate environments, but this would increase the sample size needed and increase between-operator error (greater subjectivity in scoring variables as the damage spectrum is subdivided more finely). Other studies have included specialized variables, such as root etchings and clionid borings (Parsons, 1993; Dent, 1995), cracking and peeling from subaerial exposure (Kowalewski et al., 1994), authigenic carbonate precipitation (Callender and Powell, 1992), and acquisition of diagenetic colors (from diverse mineral precipitates; Best, 2000), and these allow most effective differentiation and environmental analysis of facies. For the present sensitivity study, the most commonly used variables in taphofacies analysis were focused upon in order to make the results most broadly relevant.

CONCLUSIONS

Using the $>$8 mm portion of the bivalve death assemblage as a baseline (interior damage only, fragments included), *qualitative* trends in damage levels across the transect, as well as rank-order importance of variables within environments, are robust to most methodological variants tested here. The exceptions are insufficient sample size (to state the obvious) and, for rank order, the use of target taxa as proxies.

In contrast, and generally consistent with previous studies of some of these factors (Davies et al., 1989; Staff and Powell, 1990; Callender and Powell, 1992), the *quantitative* damage levels measured for an assemblage are significantly affected by virtually every operational decision in taphofacies analysis. These choices include size faction, sieve size, use of total rather than interior-only damage, inclusion/exclusion of fragments or of taxonomically poorly resolved specimens, focus on infauna-only, and analytic

metric, in addition to factors of larger effect (sample size and narrowing focus to target taxa). Thus, methodological artifacts in taphofacies analysis are significant for quantitative comparisons of environments, and cross-study conclusions must be made with caution unless the method is controlled (e.g., see adjustments made in size fractions, variables, metrics, and/or taxa by Callender et al., 1992, and by Kowalewski et al., 1995). To advance the field, some wider standardization of methods is desirable, as is the archiving of data in sufficiently raw form so that results can be converted.

Some disciplines have "regulated" their methodology to relatively high degrees (e.g., protocols for sieve size, sample size, and relative abundance cut-offs for "presence" in foraminiferal studies; size-fraction protocols for QFL analysis in sedimentary petrology). Self-regulation has pros and cons, among the latter being (a) adopting standards too hastily, and (b) overcoming the inertia of entrenched standards, even in the face of new information or questions (for some cautionary examples, see Martin, 1999, p.108–109, and Murray, 2000). That said, and using both present results and those of previous studies, some standardization in the treatment of size fractions would clearly be beneficial: the variance among studies has so far been huge (from 1 mm to 30 mm; Table 1), and size fraction has a significant effect on outcome, especially in settings with metazoan infestors. Because molluscan size-frequency distributions vary considerably, it is specifically recommended that, at a minimum, assemblages be analyzed in size fractions (e.g., 2–4, 4–8, etc.), rather than standardizing to a particular mesh size. This would not mean that operators "must" examine all size fractions in their samples, but that raw data should be partitioned by size fractions within the range of sizes they examine; log base-2 size-units comparable to those of sedimentology are a logical way to do this (as above). To maximize the detection of post-mortem damage, analysts could focus on larger shells (e.g., $\leq$4 mm) and include at least identifiable fragments, if not all fragments. If streamlining is necessary, high-intensity threshold damage values (e.g., % of shells in each sample falling into the maximum encrustation category) probably are more useful than average-state values or presence-absence data alone, at least when the targeted environments are quite disparate (e.g., as reef gravel v. mud in the present study). Full frequency data on damage states are obviously superior, if possible.

These methodological strategies should be relevant to analysis of skeletal remains beyond those of bivalves, and for fossil as well as modern material, although these specific effects must be tested. The issue of scoring damage to shell exteriors is narrower in relevance and unsettled. Everyone recognizes that most damage to shell exteriors is ambiguous in origin, and analyses consistently find that this damage equals or exceeds unambiguously post-mortem damage to shell interiors. However, despite the desirability of interior-only data in principle, this may well be impractical for much fossil material (but this deserves testing; e.g., Permian bivalves with internal features; Simões and Kowalewski, 1998).

Although it was not the primary purpose of this study, San Blas damage patterns indicate selectivities in taphonomic processes (see also most of the studies in Table 1). For example, post-mortem infestation is more intense in reefal shell gravel and on large shells in all environments (testable via time-lapse experiments); low-level fine-scale alteration is pervasive rather than environment-specific, implying microbial agents (testable via SEM); and fragments have the highest damage frequencies, consistent with them constituting on average older cohorts than whole shells in the same assemblage (testable via direct-dating). The differing sensitivities of target taxa to environmental conditions underscores the imprint of intrinsic biological factors on the taphonomic signatures of some taxa more than others, even within a single life-habit or shell type, and in some environments more than others. This is clearly something that can be inferred from fossil material without reference to actualistic experiments, but simply via analysis of, for example, ternary taphogram plots (cf. Fig. 13C-G). The implication of Figure 13, for example, that bivalve taxa have more disparate signatures in mud than in shell gravel is extremely tantalizing: is this unique to Ulagsuken inlet? Thus, to maximize their value to paleontologic and sedimentologic/stratigraphic investigations, actualistic taphofacies studies need broader targets than single species or genera, moving toward clade-level taphonomy and even taxon-free taphonomy (e.g., infauna versus epifauna; microstructure- or mineralogy-specific patterns).

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APPENDIX.

Ranked % abundance of species in each size fraction, and in total sample for sites 3 and 7, for all identifiable specimens (whole and fragments). Target taxa in boldface. Number of specimens indicated by n; these specimens are from splits of the total available sample for some size fractions (split indicated in parens). At site 3, the small number of specimens available in the 4–8 mm size fraction of the original sample were supplemented with specimens from two replicate samples near the same site (samples Ds116 and Ds117).

Site 3 Raw Data

%	>8 mm size fraction
20.41	***Laevicardium* cf. *L. pictum***
12.24	***Laevicardium laevigatum***
10.20	***Chlamys muscosus***
8.16	***Pitar* cf. *P. arestus***
8.16	***Chlamys* sp. 129**
4.08	*Ostrea* sp.
4.08	*Microcardium* cf. *M. perambile*
4.08	*Macominae* cf. *Macoma tageliformis*
4.08	*Dosinia concentrica*
2.04	*Pinna attenuata*
2.04	*Americardia* cf. *A. media*
2.04	*Tagelus* cf. *T plebeius*
2.04	***Pecten* ss. cf. *P. chazelisi?***
2.04	*Amusium* sp.
2.04	***Pitar* sp. 70**
2.04	*Codakia* sp. 74
2.04	*Cyclinella tenuis*
2.04	thraciid cf. *Cyathodonta semirugosa*
2.04	*Lima lima*
2.04	*mactrid cf. Mactra*
2.04	*Tellina* (*Angulus*) sp. 139
	n = 49 (entire sample used)

%	4–8 mm size fraction
27.27	*Nuculana acuta*
18.18	***Laevicardium pictum***
9.09	***Laevicardium laevigatum***
9.09	*Corbula caribaea*
9.09	*Codakia* (*Ctena*) sp.
9.09	*Dosinia concentrica*
9.09	**pectinid**
9.09	tellinid
	n = 11 (entire sample used)

%	2–4 mm size fraction
19.77	**Pitar sp. 70**
13.95	***Laevicardium* sp.**
12.79	***Chlamys muscosus***
6.98	**pectinid**
5.81	*Nuculana acuta*
5.81	***Chlamys* sp. 129**
4.65	*Corbula caribaea*
3.49	*Codakia* (*Ctena*) sp.
3.49	*Barbatia* sp. 141
2.33	*Tellina* (*Angulus*) *probina*
2.33	*Tellina* (*Angulus*) *euvitrea*
2.33	*Papyridea* cf. *P. soleniformis*
2.33	***Pitar* cf. *P. fulminatus***
2.33	*Corbula* (*Varicorbula*) sp. indet.
1.16	*Tellina* (*Angulus*) sp.
1.16	*Trachycardium* cf. *T. muricatum*
1.16	*Anadara tricenicostata*?
1.16	*Americardia* cf. *A. media*
1.16	*Cardiomya* 2 spp
1.16	*Nuculana acuta*
1.16	thraciid cf. *Cyathodonta semirugosa*
1.16	*Lepton* sp. indet.
1.16	*Nucula dalmasi*
1.16	arcid
	n = 86 (1/8 of sample used)

APPENDIX.

Continued.

Supplement from Sample DS116

%	4–8 mm
12.77	***Laevicardium* sp.**
11.70	***Pitar* sp. 70**
9.57	***Chlamys* sp. 129**
7.45	***Chlamys muscosus***
6.38	***Chlamys* group**
6.38	***Laevicardium* cf. *L. pictum***
5.32	*Americardia* cf. *A. media*
5.32	**pectinid**
4.26	*Papyridea* cf. *P. soleniformis*
3.19	thraciid cf. *Cyathodonta semirugosa*
2.13	*Chama congregata*
2.13	*Corbula caribaea*
2.13	mactrid cf. *Mactra*
2.13	pteriid
2.13	*Diplodonta* cf. *D.* (*Phlyctiderma*) *notata*
2.13	arcid
2.13	tellinid
1.06	*Nuculana acuta*
1.06	*Ostrea* sp.
1.06	*Anadara tricenicostata?*
1.06	*Tellina* (*Angulus*) *probina*
1.06	*Arca* cf. *A. imbricata*
1.06	*Dosinia concentrica*
1.06	***Laevicardium pictum***
1.06	*Anadara* sp. 119
1.06	*Plicatula* sp. 134
1.06	***Lyropecten* sp.**
1.06	*Tellina* cf. *T.* (Tellinella)
1.06	mytilid
	n = 94 (1/2 of sample used)

Supplement from Sample Ds117

%	4–8 mm
22.86	***Pitar* sp. 70**
11.43	***Laevicardium* sp.**
7.86	***Chlamys muscosus***
5.71	***Chlamys* sp. 129**
5.00	thraciid cf. *Cyathodonta semirugosa*
3.57	*Papyridea* cf. *P. soleniformis*
3.57	mactrid cf. *Mactra*
3.57	*Tellina* (*Merisca*) sp.
2.86	***Laevicardium* cf. *L. pictum***
2.86	*Americardia* cf. *A. media*
2.86	***Laevicardium pictum***
2.86	**pectinid**
2.14	*Corbula caribaea*
2.14	*Codakia* (*Ctena*) sp.
1.43	*Nuculana acuta*
1.43	*Chama congregata*
1.43	*Lima scabra tenera*
1.43	pteriid
1.43	***Lyropecten* sp.**
1.43	arcid
1.43	chamid
0.71	*Ostrea* sp.
0.71	*Tellina* (*Angulus*) *probina*
0.71	*Chama macerophylla*
0.71	*Arca* cf. *A. imbricata*
0.71	*Corbula* (*Juliacorbula*) *aequivalvis*
0.71	*Isognomon* sp.
0.71	***Pitar* cf. *P. fulminatus***
0.71	*Arca* cf. *A. zebra*
0.71	*Barbatia* sp. 118
0.71	*Anadara* sp. 119
0.71	*Chione paphia*
0.71	***Chlamys* sp. 142**
0.71	*Periglypta* cf. *P. listeri*
0.71	*Diplodonta* cf. *D.* (*Phylctiderma*) *notata*
0.71	tellinid
	n = 140 (1/4 of sample used)

APPENDIX.

Continued.

%	Total data for site 3
15.80	***Pitar* sp. 70**
10.36	***Laevicardium* sp.**
8.81	***Chlamys muscosus***
5.18	***Laevicardium* cf. *L. pictum***
4.40	***Chlamys* sp. 129**
4.15	**pectinid**
3.37	pteriid
3.11	*Nuculana acuta*
3.11	thraciid cf. *Cyathodonta semirugosa*
2.85	*Americardia* cf. *A. media*
2.85	*Papyridea* cf. *P. soleniformis*
2.59	*Corbula caribaea*
2.59	*Ostrea* sp.
2.07	mactrid cf. *Mactra*
1.81	***Laevicardium laevigatum***
1.81	*Codakia* (*Ctena*) sp.
1.81	***Laevicardium pictum***
1.55	***Chlamys* group**
1.30	*Tellina* (*Merisca*) sp.
1.30	arcid
1.04	*Chama congregata*
1.04	***Pitar* cf. *P. arestus***
1.04	*Tellina* (*Angulus*) *probina*
1.04	*Dosinia concentrica*
1.04	tellinid
0.78	***Pitar* cf. *P. fulminatus***
0.78	*Barbatia* sp. 141
0.78	***Lyropecten* sp.**
0.52	*Anadara tricenicostata?*
0.52	*Microcardium* cf. *M. perambile*
0.52	*Lima scabra tenera*
0.52	*Tellina* (*Angulus*) *euvitrea*
0.52	*Arca* cf. *A. imbricata*
0.52	Macominae cf. *Macoma tageliformis*
0.52	*Anadara* sp. 119
0.52	*Diplodenta* cf. *D.* (*Phlytiderma*) *notata*
0.52	*Corbula* (*Varicorbula*) sp. indet.
0.52	chamid
0.26	*Pinna attenuata*
0.26	*Tellina* (*Angulus*) sp.
0.26	*Trachycardium* cf. *T. muricatum*
0.26	*Chama macerophylla*
0.26	*Tagelus* cf. *T. plebeius*
0.26	*Cardiomya* 2 spp.
0.26	***Pecten* ss. cf. *P. chazelisi?***
0.26	*Amusium* sp.
0.26	*Corbula* (*Juliacorbula*) *aequivalvis*
0.26	*Codakia* sp. 74
0.26	*Isognomon* sp.
0.26	*Cyclinella tenuis*
0.26	*Lima lima*
0.26	*Arca* cf. *A. zebra*
0.26	*Barbatia* sp. 118
0.26	*Chione paphia*
0.26	*Plicatula* sp. 134
0.26	*Tellina* (*Angulus*) sp. 139
0.26	***Chlamys* sp. 142**
0.26	*Periglypta* cf. *P. listeri*
0.26	*Tellina* cf. *T.* (*Tellinella*)
0.26	mytilid
0.26	*Diplodonta* cf. *D.* (*Phylctiderma*) *notata*
0.26	*Lepton* sp. indet.
0.26	*Nucula dalmasi*
	n = 386

APPENDIX.

Continued.

%	Site 7 Raw Data >8 mm size fraction
8.88	*Americardia* cf. *A. media*
8.22	**pectinid**
7.89	***Laevicardium laevigatum***
7.89	arcid
6.58	*Papyridea* cf. *P. soleniformis*
6.58	***Chlamys* sp. 129**
6.09	*Chama macerophylla*
4.93	mactrid cf. *Mactra*
4.61	***Chlamys muscosus***
3.78	***Laevicardium*** sp.
2.80	*Lima scabra*
2.63	***Chlamys* group**
2.47	*Chama congregata*
2.14	***Pitar* sp. 70**
2.14	pteriid
1.81	*Anadara notabilis*
1.64	mactrid
1.48	***Laevicardium* cf. *L. pictum***
1.48	*Arca* cf. *A. imbricata*
1.32	*Lima scabra tenera*
1.32	***Pitar* cf. *P. fulminatus***
1.15	*Arca* sp. 117
0.99	*Barbatia* sp. 32
0.99	*Barbatia* sp. 115
0.82	chamid
0.66	*Macoma* sp. cf. *M. tageliformis*
0.49	*Pinna attenuata*
0.49	*Anadara* (*Cunearca*) *brasiliana*
0.49	Macominae cf. *Macoma tageliformis*
0.49	*Arca* cf. *A. zebra*
0.49	*Anadara* cf. *A. notabilis*
0.49	*Pododesma rudis*
0.33	*Ostrea* sp.
0.33	***Pitar* cf. *P. arestus***
0.33	*Microcardium* cf. *M. perambile*
0.33	*Lithophaga* sp.
0.33	*Cyclinella tenuis*
0.33	*Codakia* (*Ctena*) *orbiculata*
0.33	*Barbatia* sp. 118
0.33	limid
0.16	*Trachycardium* cf. *T. muricatum*
0.16	*Corbula caribaea*
0.16	*Diplodonta* sp. cf. *D. punctata*
0.16	*Tellina* (*Eurytellina*) *nitens*
0.16	*Tellina* (*Arcopagia***)** *fausta*
0.16	*Isognomon* sp.
0.16	*Callista* (*Macrocallista*) sp. cf. *C. maculata*
0.16	lucinid
0.16	*Lopha frons*
0.16	*Tagelus* cf. *T. plebeius*
0.16	*Codakia* (*Ctena*) sp.
0.16	***Laevicardium pictum***
0.16	*Anadara* sp. 119
0.16	*Tellina* (*Merisca*) sp.
0.16	cardiid
0.16	Plicatula sp. 134
0.16	**Chlamys sp. 135**
0.16	*Tellina* (*Angulus*) sp. 139
0.16	tellinid
	n = 608 (entire sample used)

APPENDIX.

Continued.

%	4–8 mm size fraction
6.25	*Chama congregata*
6.25	*Lima scabra tenera*
6.25	*Arca* cf. *A. imbricata*
6.25	pteriid
5	*Pinna attenuata*
5	*Barbatia* sp. 32
5	***Laevicardium* cf. *L. laevigatum***
3.75	*Trachycardium* cf. *T. muricatum*
3.75	*Corbula caribaea*
3.75	*Anadara* sp. 119
2.5	*Lithophaga* sp.
2.5	*Lopha frons*
2.5	*Barbatia* sp. 115
2.5	*Lima* cf. *L. pellucida*
2.5	*Barbatia* sp. 141
2.5	*Periglypta* cf. *P. listeri*
1.25	***Laevicardium laevigatum***
1.25	*Chione cancellata?*
1.25	*Ostrea* sp.
1.25	***Chlamys* group**
1.25	*Americardia* cf. *A. media*
1.25	*Chama macerophylla*
1.25	***Pitar* sp. 70**
1.25	*Isognomon* sp.
1.25	*Lima scabra*
1.25	*Papyridea* cf. *P. soleniformis*
1.25	*Anadara notabilis*
1.25	***Pitar* cf. *P. fulminatus***
1.25	*Lima lima*
1.25	*Codakia* (*Ctena*) sp.
1.25	mactrid cf. *Mactra*
1.25	*Solecurtus* sp. cf. *S. cumingianus*
1.25	***Chlamys muscosus***
1.25	***Chlamys* sp. 129**
1.25	cardiid
1.25	*Tellina* (*Angulus*) sp. 139
1.25	*Barbatia* sp. 140
1.25	***Chlamys* sp. 142**
1.25	***Lyropecten* sp.**
1.25	arcid
1.25	**pectinid**
1.25	***Laevicardium* sp.**
1.25	tellinid
	n = 80 (1/4 of sample used)

%	2–4 mm size fraction
31.65	***Pitar* sp. 70**
12.66	***Laevicardium* sp.**
7.59	*Papyridea* cf. *P. soleniformis*
7.59	mactrid cf. *Mactra*
7.59	***Chlamys muscosus***
6.33	*Corbula caribaea*
5.06	*Codakia* (*Ctena*) sp.
5.06	*Barbatia* sp. 141
2.53	*Barbatia* sp. 115
2.53	*Crassinella* sp. 149
2.53	arcid
1.27	*Tellina* (*Scisulla*) *similis*
1.27	*Barbatia* sp. 118
1.27	pteriid
1.27	***Chlamys* sp. 129**
1.27	***Lyropecten* sp.**
1.27	**pectinid**
1.27	chamid
	n = 79 (1/32 of sample used)

APPENDIX.

Continued.

%	Total data for site 7
7.17	*Americardia* cf. *A. media*
6.78	**pectinid**
6.65	arcid
6.39	***Laevicardium laevigatum***
6.13	*Papyridea* cf. *P. soleniformis*
5.48	***Chlamys* sp. 129**
5.08	***Pitar* sp. 70**
4.95	*Chama macerophylla*
4.82	mactrid cf. *Mactra*
4.56	***Chlamys muscosus***
4.43	***Laevicardium* sp.**
2.61	*Chama congregata*
2.48	pteriid
2.35	*Lima scabra*
2.22	***Chlamys* group**
1.83	*Arca* cf. *A. imbricata*
1.69	*Lima scabra tenera*
1.56	*Anadara notabilis*
1.30	*Barbatia* sp. 32
1.30	*Barbatia* sp. 115
1.30	mactrid
1.17	*Corbula caribaea*
1.17	***Laevicardium* cf. *L. pictum***
1.17	***Pitar* cf. *P. fulminatus***
0.91	*Pinna attenuata*
0.91	*Arca* sp. 117
0.78	*Codakia* (*Ctena*) sp.
0.78	*Barbatia* sp. 141
0.65	chamid
0.52	*Trachycardium* cf. *T. muricatum*
0.52	*Lithophaga* sp.
0.52	***Laevicardium* cf. *L. laevigatum***
0.52	*Anadara* sp. 119
0.52	*Macoma* sp. cf. *M. tageliformis*
0.39	*Ostrea* sp.
0.39	*Anadara* (*Cunearca*) *brasiliana*
0.39	*Lopha frons*
0.39	*Macominae* cf. *Macoma tageliformis*
0.39	*Arca* cf. *A. zebra*
0.39	*Barbatia* sp. 118
0.39	*Anadara* cf. *A. notabilis*
0.39	*Pododesma rudis*
0.39	tellinid
0.26	***Pitar* cf. *P. arestus***
0.26	*Microcardium* cf. *M. perambile*
0.26	*Isognomon* sp.
0.26	*Cyclinella tenuis*
0.26	*Codakia* (*Ctena*) *orbiculata*
0.26	*Lima* cf. *L. pellucida*
0.26	cardiid
0.26	*Telina* (*Angulus*) sp. 139
0.26	***Lyropecten* sp.**
0.26	*Periglypta* cf. *P. listeri*
0.26	*Crassinella* sp. 149
0.26	limid
0.13	*Chione cancellata?*
0.13	*Diplodonta* sp. cf. *D. punctata*
0.13	*Tellina* (*Eurytellina*) *nitens*
0.13	*Tellina* (*Arcopagia*) *fausta*
0.13	*Callista* (*Macrocallista*) sp. cf. *C. maculata*
0.13	lucinid
0.13	*Tagelus* cf. *T. plebeius*
0.13	*Lima lima*
0.13	*Tellina* (*Scisulla*) *similis*
0.13	***Laevicardium pictum***
0.13	*Solecurtus* sp. cf. *S. cumingianus*
0.13	*Tellina* (*Merisca*) sp.
0.13	*Plicatula* sp. 134
0.13	***Chlamys* sp. 135**
0.13	*Barbatia* sp. 140
0.13	***Chlamys* sp. 142**
	n = 767